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LXI. A METHOD FOR THE CALCULATION OF THE GROWTH OF  
FISHES FROM SCALE MEASUREMENTS, by F. E. J. FRY

LXII. THE WHITEFISH, *COREGONUS CLUPEAFORMIS* (MITCHILL), OF LAKE  
OPEONGO, ALGONQUIN PARK, ONTARIO, by W. A. KENNEDY

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# A METHOD FOR THE CALCULATION OF THE GROWTH OF FISHES FROM SCALE MEASUREMENTS

By


F. E. J. FRY

(From the Department of Zoology,  
University of Toronto)



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# A METHOD FOR THE CALCULATION OF THE GROWTH OF FISHES FROM SCALE MEASUREMENTS

## ABSTRACT

Huxley's formula for heterogonic growth appears to fit the scale/body length relationship in fish when a correction is made for the growth of the fish previous to the laying down of the scale. Demonstrations of the applicability of the formula are given in the form of plots of scale/body relationships on a double logarithmic grid. A calculator for obtaining fish lengths from scale measurements is described which applies Huxley's formula for heterogonic growth.

## INTRODUCTION

An application of Huxley's formula for heterogonic growth to the scale/body relationship in fishes is introduced here. There is also a description of a calculator that makes use of this formula in the calculation of the size of fishes corresponding to diameters of the annuli of their scales laid down in the years of their existence previous to capture.

The excellent reviews of Graham (1928), Van Oosten (1929), and Lee (1920) render idle any discussion here of the history and applications of the scale method to growth calculations. However, mention should be made of the logarithmic formula introduced by Monastuirsky (1926) which differs from the one proposed here only in that it makes no allowance for the length attained by the fish before the scale is laid down.

Huxley (1932) has shown that the many cases of differential growth which he investigated could be expressed by one general formula which may be written as:—

$$y = bx^a$$

where  $y$  is a dimension of one part

$x$  is a dimension of the other part minus any dimension it might have had at the inception of part " $y$ "

$b$  and  $a$  are constants.

The logarithmic form of this equation:—

$$\log y = a \log x + \log b,$$

gives a straight line in those cases where the constants " $a$ " and " $b$ " remain the same throughout the life of the organism. This

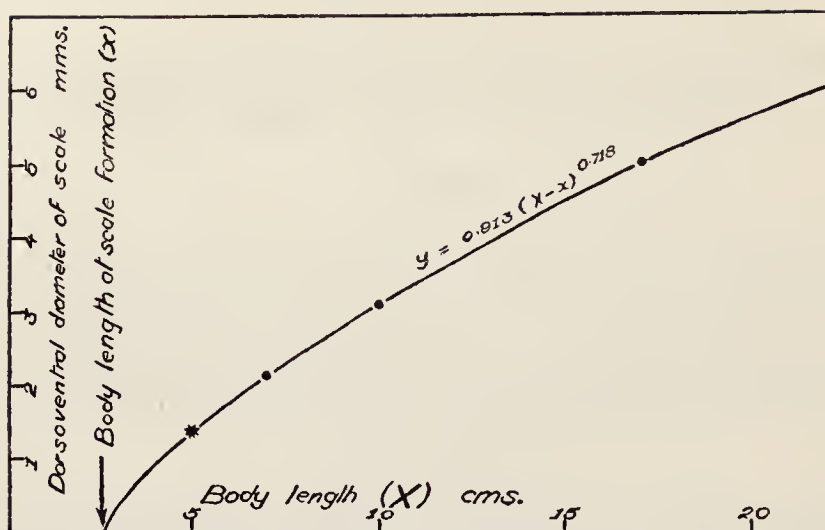


FIGURE 1.—The relation between dorso-ventral diameter of the scale and body length in *Pomolobus pseudoharengus*. Data from Huntsman, 1918.  $x = 2.5$  cm.

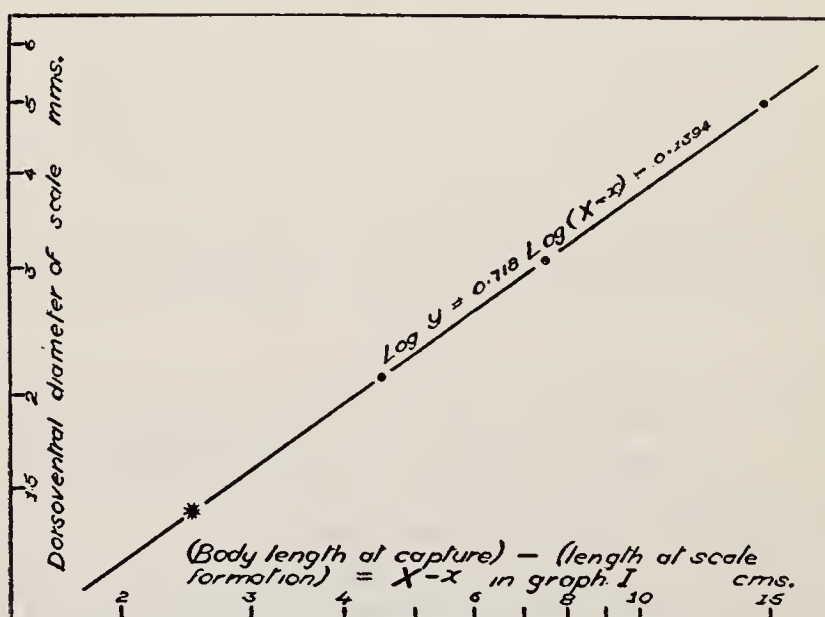


FIGURE 2.—The same data as in figure 1 plotted on a logarithmic scale.

appears to be the nature of the relation existing between growth of the scales and of the body in fishes.

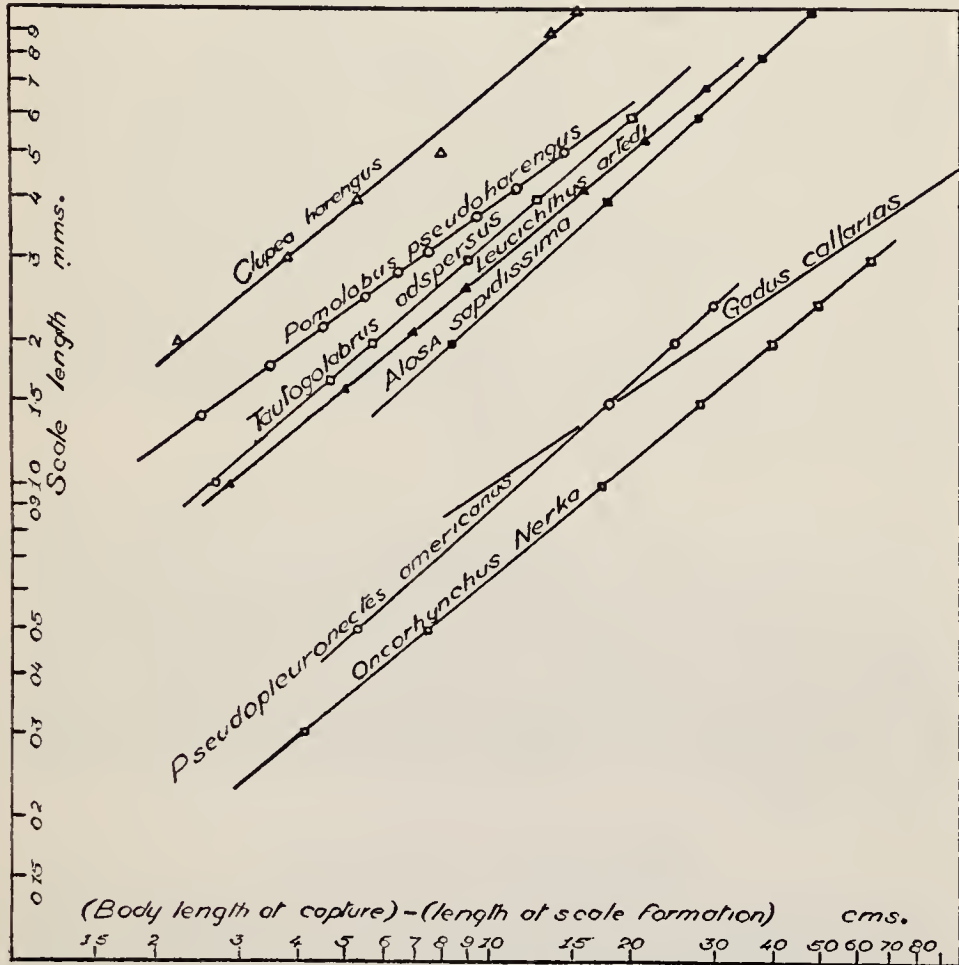


FIGURE 3.—The logarithmic relationship in various species. For sources of data see text.

Figure 1, taken from Huntsman (1918), fig. 11, which shows the relation between a linear dimension of "side" scales and the standard length of the body in *Pomolobus pseudoharengus*, may be taken as an illustration of a curve fulfilling the arithmetical form of the equation. From the information afforded by figure 1, figure 2 has been plotted on logarithmic paper, the length of the body at the time of scale formation being the point where the curve in figure 1 cuts the "x" axis. Figure 3 gives further examples of

the relationship in its logarithmic form plotted from data presented in various papers. The data for *Clupea harengus*, *Tautoglabrus adspersus*, and *Pseudopleuronectes americanus* were taken from Huntsman (1918), for *Alosa sapidissima* from a curve given in Leim (1924), for *Oncorhynchus nerka* from Dunlop (1924), for *Gadus callarius* from the measurements by Duff (1929), and for the lake Huron race of *Leucichthys artedi* from Van Oosten (1929). In most cases surprisingly good approximations to straight lines have resulted, the greatest divergence being at one point in the curve for *Clupea harengus* at a place where the line had apparently been drawn slightly askew. It should be noted, too, that many of these curves include measurements made on quite small fish so that extrapolation has not played an unduly great part in the derivation of the logarithmic lines.

#### ACKNOWLEDGMENTS

This work has been carried on in the Ontario Fisheries Research Laboratory of the Department of Zoology of the University of Toronto, under the direction of Professors J. R. Dymond and W. J. K. Harkness. I wish to acknowledge my indebtedness to Mr. E. W. Skelton for his assistance in working out the application of the formula.

#### DESCRIPTION OF APPARATUS

The apparatus is based on the following principles. If two arithmetic series are compared on ordinary graph paper a straight line will result, and the two series may be compared according to the principle of similar triangles on a proportionality machine such as is described in Lea (1915). This is constructed as shown in figure 4. To use this the movable arm is swung on its pivot until its edge coincides with "x", a chosen point on one series. The other series is placed on a vertical, moving scale and slid along the baseline until the corresponding point " $x_1$ " coincides with the edge of the arm. Swinging the arm now cuts off proportional intervals on the two scales.

Similarly two series which give a straight line when plotted

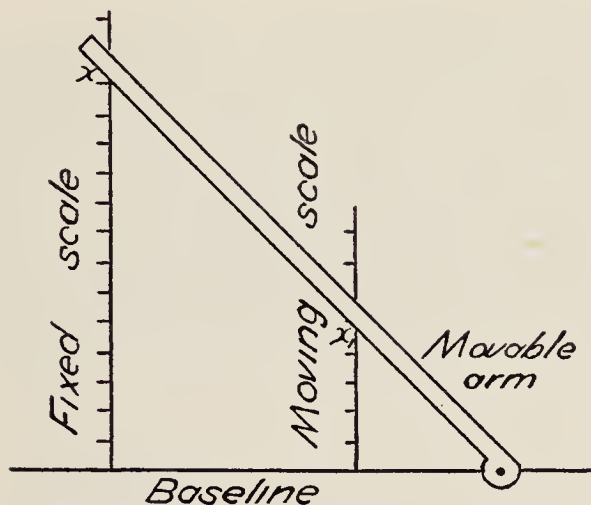


FIGURE 4

against each other on logarithmic paper may be compared on a proportionality machine if the fixed and moving scales be divided into logarithmic instead of arithmetic units.

Now the case of the arithmetic series discussed in the paragraph above is a particular case involving two series starting out simultaneously from zero. In all other cases the base line has to cut the fixed and moving scales at points which correspond with one set of values fulfilling the ratio between the series under comparison.

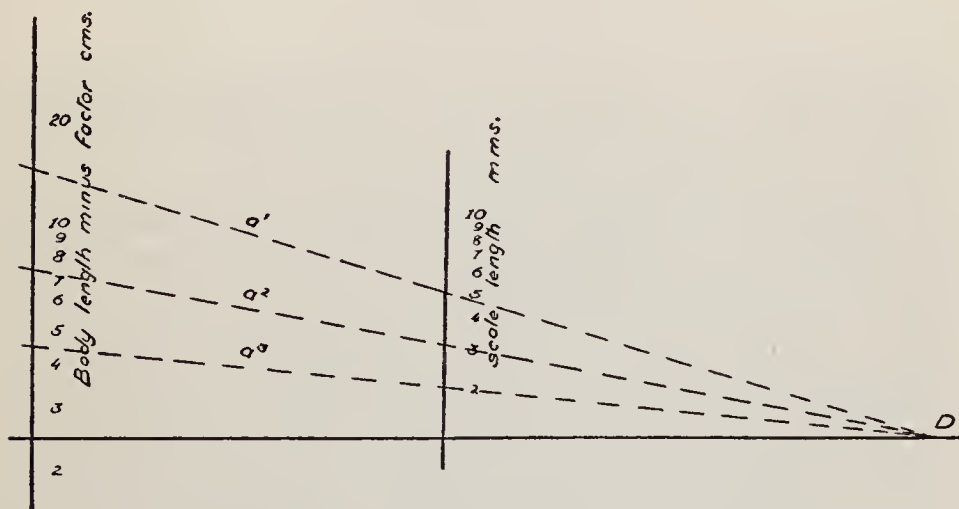


FIGURE 5

This is always so when logarithmic scales are being dealt with, for log. zero is minus infinity. This may perhaps best be made clear by an example. Figure 5 shows the relation of the scales with respect to the body with baseline set to fit the case of *Pomolobus pseudoharengus* illustrated in figures 1 and 2. In this instance the baseline cuts the "scale diameter" scale at 1.4 mm. and the "body length attained since scale formation" scale at 2.5 cm. This point is indicated on the graphs by an asterisk. Lines "a<sup>1</sup>", "a<sup>2</sup>", and "a<sup>3</sup>" illustrate positions of the hairline pivoted at "D" which

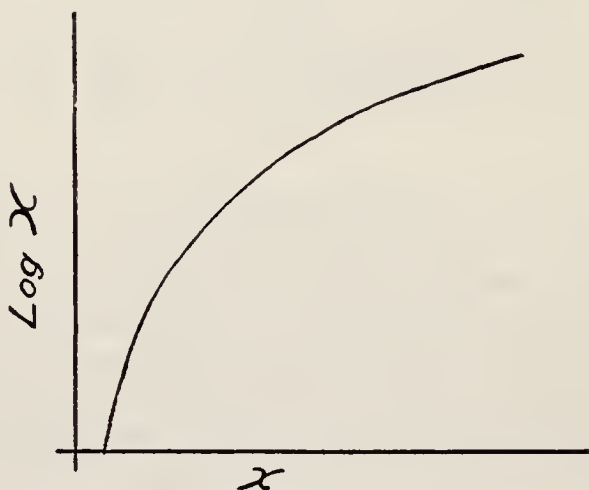


FIGURE 6

cut off points on the two scales having values corresponding to those of the solid dots shown on figures 1 and 2.

It is possible, then, by choosing a suitable scale, to compare by proportions two series whose logarithms give a straight line relationship. The evidence submitted in the introduction indicates that fish scale and body growth conform to such a relationship. It remains only, then, to get a magnification of a fish scale in logarithmic units. To do this it is necessary to turn the projected image from its normal arithmetic scale into a logarithmic one by some graphical method. Such a curve is plotted in figure 6.

To avoid having to use a multiplicity of such curves and to be able to use within limits any convenient magnification, a second



proportionality machine is used that reduces images to a definite magnification. In the case of the apparatus described this magnification is 20 diameters. This proportionality machine works in the following manner (see figure 7). "A" is a fixed scale erected at "O" at right angles to the baseline "OD". "B" is a moving arm pivoted at "D" so that a hairline along "B" swings about "D". The line "OD" is divided into 20 equal divisions. Now if a

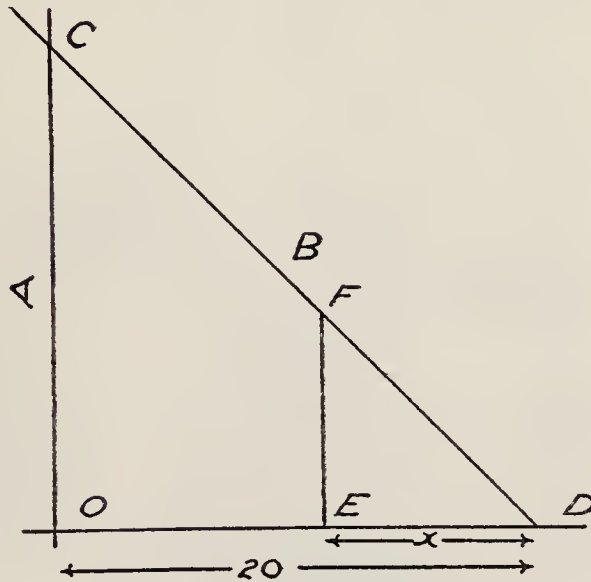


FIGURE 7

perpendicular be erected at "E" a distance of " $x$ " units from "D", the distance "EF" above the baseline, that is cut off along it by the hairline, is to "CO", the distance cut off along "A" by the hairline, as " $x$ " is to 20. Accordingly if "EF" be " $x$ " times the natural dimension of a length then "CO" will be the natural dimension magnified by 20 diameters and it follows as a corollary that if an image of known magnification be erected at the unit along "OD" corresponding to this magnification it may be magnified to 20 diameters on the scale "A", and if "CO" be divided into units 20 times a natural dimension the natural size may be read directly on it.

Now if "A" be used as the abscissa of a graph showing the relationship between " $x$ " and  $\log. "x"$  then the logarithm of " $x$ "

can be read off along " $OM$ " or in effect, " $OM$ " is a logarithmic scale (figure 8). Then by pivoting an arm similar to " $B$ " on " $A$ " at " $C_1$ " the scale on " $OM$ " could be compared with another logarithmic scale ( $O_1M_1$ ) as in figure 9.

To be able to compare different series, the scale " $MO$ " must be

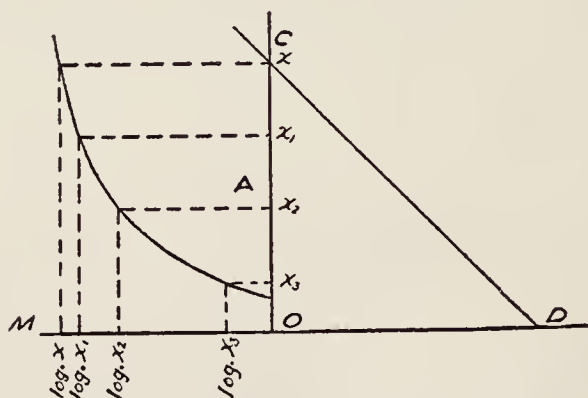


FIGURE 8

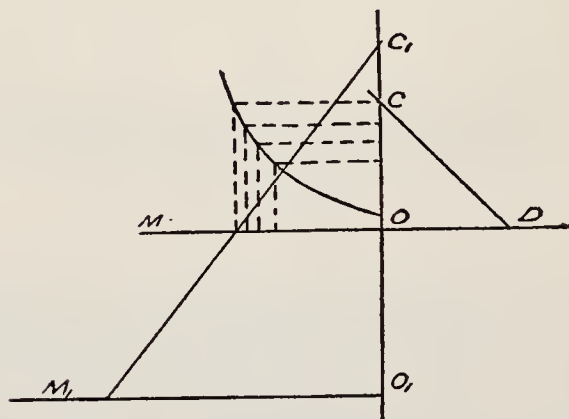


FIGURE 9

able to change its position with respect to " $C_1$ " and " $O_1$ ", and the baseline " $C_1O_1$ " must be shifted along the scales " $MO$ " and " $M_1O_1$ ".

These principles have been incorporated in the apparatus in the following manner. The arrangement of the two proportionality machines, and the log. curve is shown in the sketch given with the plan of the apparatus. This sketch is lettered as in figures



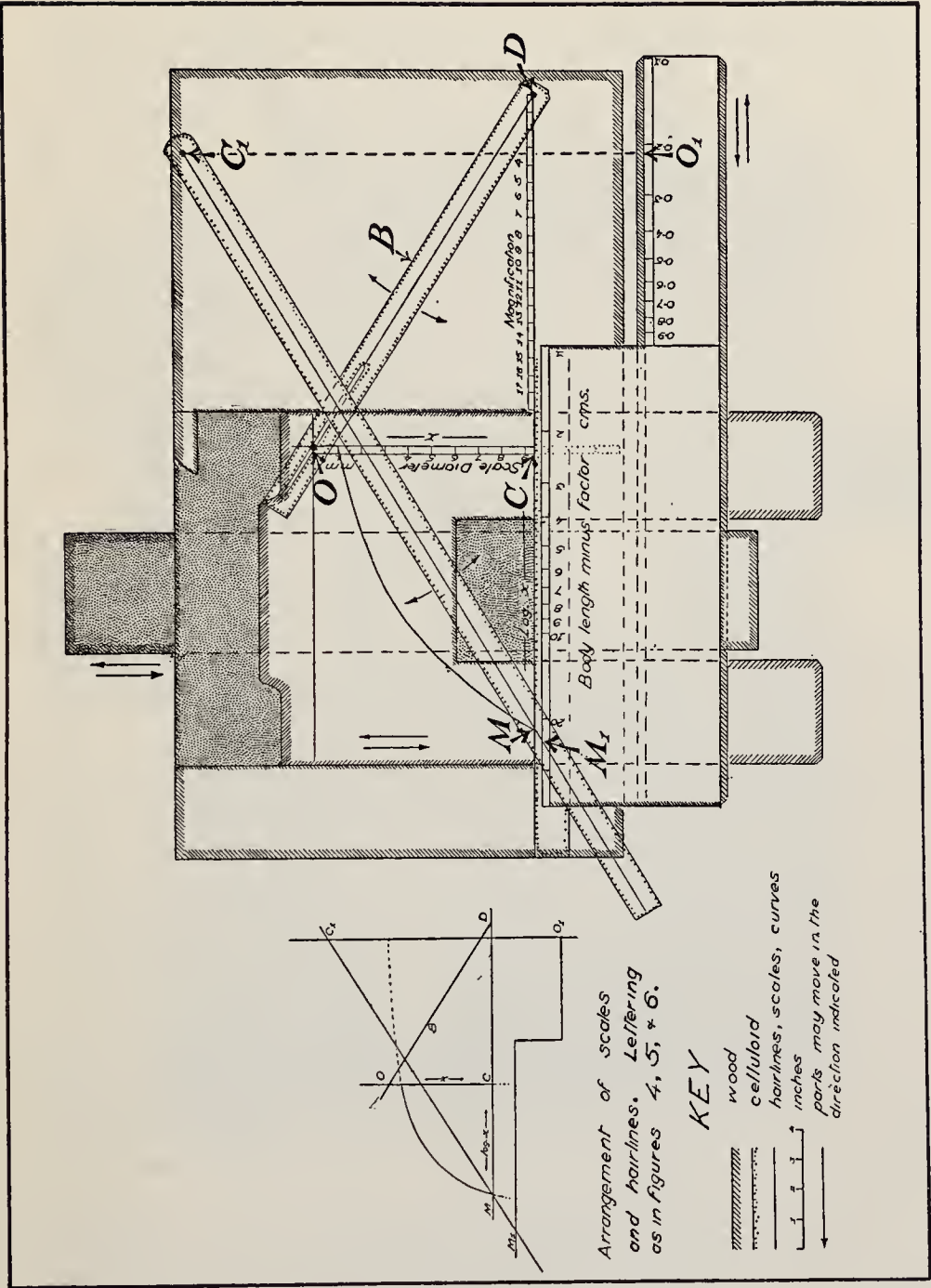


FIGURE 10.—Plan of apparatus.

7, 8, and 9. A study of it will show several modifications of the relations shown in figure 9. The baseline " $OC$ " of the log. curve has been laterally inverted and the point " $O$ " is shackled to the arm " $B$ ". The curve is so mounted that it may pass under the line " $MD$ ". The point where the curve cuts the line " $MD$ " is the logarithm of the distance " $OC$ ". The position of the scale " $MO$ ", figure 9, with respect to the point " $C_1$ " has been fixed, and the point where it cuts the baseline has also been fixed at log. 0.1 mm. The first cycle (0.1 to 1.0) of the curve above the baseline has been omitted and the space used to accommodate the part of the apparatus used for obtaining a standard magnification (see figure 7). The scale " $M_1O_1$ " on which body length is read has a step in it that leaves a free space between " $C$ " and " $D$ ". The distance between " $C_1$ " and " $O_1$ " may be varied and the height of " $M_1$ " above " $O_1$ " may also be varied.

#### OPERATION

The scales are projected on to filing cards after the manner described by Lea (1915). A number of scales of fishes of different sizes, taken from a particular region of the body, are measured, the measurement taken being dependent on the species. For cycloid scales a diameter would be used, in the case of fishes with ctenoid scales, the anterior radius would be measured. These data are used to plot a curve between scale size and body length as was plotted in figure 1. From this graph the average size of the fish at time of scale formation can be obtained by extrapolation. The same material is then plotted on logarithmic paper using this time "body length minus length at time of scale formation." This should give a straight line as in figure 2. It may be necessary to add to or subtract from the first extrapolated value for a size of fish at scale formation to get a straight line. This straight line is then extrapolated so that the amount the fish has grown since the formation of the scale while the scale has been attaining the length of 0.1 mm. may be read.

The scale " $M_1O_1$ " is moved perpendicular to " $C_1O_1$ " until the point read at " $O_1$ " is the size of the fish attained since scale formation corresponding to a scale length of 0.1 mm. " $M_1O_1$ " is then

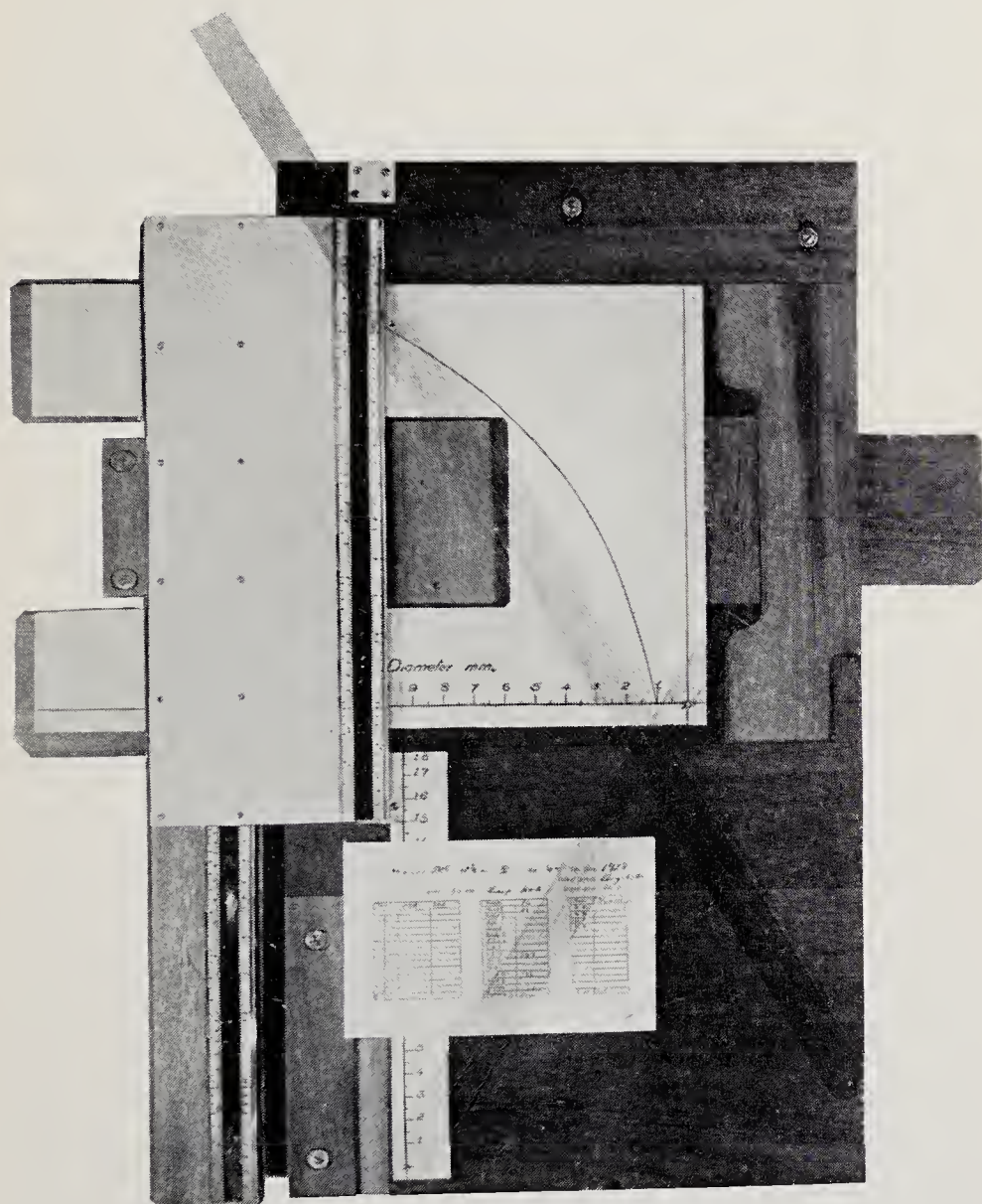


FIGURE 11.—Photograph of apparatus.





locked in this position. A card with scale measurements projected along its edge is erected perpendicular to " $CD$ " with the edge on which the image has been projected at the unit on " $CD$ " corresponding to its magnification. The lower boundary of the image is placed on the line " $CD$ ". " $B$ " is swung down until the hairline cuts the edge of the card at the upper boundary of the image, moving the log. curve with it. The arm " $C_1M_1$ " is swung down until its hairline lies over the point " $M$ " where the log. curve cuts the line " $MCD$ ", then the point " $O_1$ " is approached to or withdrawn from " $C_1$ " until " $C$ ", " $M$ ", and the length of the fish minus the average length at scale formation, " $M_1$ ", are in line.

To read the fish length then at the end of year " $x$ " the card with the image on it is slipped down until the lower boundary of this annulus is on " $MCD$ ". " $B$ " is swung down until the hairline touches the upper boundary, " $O$ " follows the hairline. The arm " $C_1M_1$ " is swung down so that the hairline on it cuts " $MC$ " at the same point as the log. curve does in its new position. On " $M_1O_1$ " may then be read the length of the fish attained since the time of scale formation. The true length of the fish is arrived at by adding to this figure the amount that represents the growth attained before the scale is formed.

The setting of the scale " $M_1O_1$ " by moving it perpendicular to " $C_1O_1$ " is made only once for a given species or race. Movement of the point " $O_1$ " with respect to " $C_1$ " is made once for each scale from which calculations are made.

This apparatus was first used to make an assessment of the growth history of the Lake Nipissing cisco (Fry, 1937, pp. 63 ff.). A particular study was made of the male fish taken at one particular station in three successive years. It was found that (table 18, Fry, 1937) regardless of the age of the fish when captured the calculated values for the length of the fish at the formation of the first annulus, in a given year class, agree within the limits of probable error. Calculations at subsequent annuli showed Lee's phenomenon but there is evidence to indicate that the phenomenon in this instance represents a real difference in the growth rate of individuals making up the sample in different years.

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# THE WHITEFISH, *COREGONUS CLUPEAFORMIS* (MITCHILL), OF LAKE OPEONGO, ALGONQUIN PARK, ONTARIO

By  
W. A. KENNEDY  
(From the Department of Biology  
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# THE WHITEFISH, *COREGONUS CLUPEAFORMIS* (MITCHILL), OF LAKE OPEONGO, ALGONQUIN PARK, ONTARIO

## ABSTRACT

In lake Opeongo, Algonquin Park, Ontario, are found two groups of the whitefish, *Coregonus clupeaformis* (Mitchill), which are distinguished from each other by the size at which they mature, both sexes being about equally represented in each group. The size distribution of mature individuals is bimodal, the modes coming at 120 mm. and 240 mm. The trough between the modes occurs at 150 mm.

Slight but significant differences in numbers of scales and gill rakers between the two groups were observed, but no differences between body measurements were found, other than those resulting from size differences.

Individuals of the small-sized group are further distinguished from those of the large-sized group by the fact that they grow more slowly and for a shorter season, mature when younger, and live for a shorter time.

The difference between the two groups is not considered to be the result of environment because no outstanding difference was found in vertical distribution during the growing season.

In the growth studies, no evidence was found of Lee's phenomenon nor of the law of compensation of growth.

## INTRODUCTION

The present problem arose during the summer of 1938 when members of the Ontario Fisheries Research Laboratory found a rather unusual situation among the whitefish, *Coregonus clupeaformis* (Mitchill), of lake Opeongo. The whitefish there showed a surprising diversity in the size at which they became mature. Some mature fish weighed only 18 grams, while one specimen weighed as much as 1,980 grams.

The size range was so great that it raised the question as to whether this was the normal variation of size in a homogeneous population, or whether there were actually more than one group of whitefish present which matured at different sizes.

In several other species of fish, cases have been found in which there are two populations distinguished from each other principally by the size at which they mature. A few examples follow:

Greene (1930) found among the smelts, *Osmerus mordax* (Mitch-

ill), of lake Champlain, two quite distinct size groups which he considers to be physiologically distinct from each other. He says: "However, a careful analysis with the hope of finding an anatomical basis on which to separate the two has been singularly unfruitful." He concludes that the two groups are genetically distinct.

Dymond (personal communication) reported two forms of the kokanee, *Oncorhynchus nerka kennerlyi* Suckley, of the Shuswap region, B.C. "In this area the smaller form is said not to spawn until the larger form has been spawning some time. The smaller ones are said to be less numerous and to be of a different colour at spawning time."

In the Catostomidae, subspecies which are distinguished by size at maturity have been recognized. Dence (1937) found common suckers, *Catostomus commersonnii commersonnii* (Lacépède), to mature when 12-18 inches long, whereas in the same waters dwarf common suckers, *Catostomus commersonnii utawana* (Mather), mature when only 5-8 inches long. Greeley and Greene (1931) and Greeley and Bishop (1932) recognize these two subspecies but find intergradations between them. Kennedy (MS) has shown bimodality among the common suckers of Whitetrout lake, Algonquin Park, Ontario. However, he did not find as complete a separation between the two groups as did Dence.

Two sub-species are also recognized among the northern suckers on the basis of size. *Catostomus catostomus catostomus* (Forster) is the common form while *Catostomus catostomus nannomyzon* Mather is a rarer form regarded as a dwarf sub-species. Greeley and Bishop (1932) list as points in which the dwarf differs from the larger form: ". . . (1) smaller size at maturity (2) heavier tuberculation of breeding fish, the females having pearl organs nearly as well developed as males; the latter having them much better developed than males of *catostomus* (3) shorter head length (4) longer fins . . . ."

Early in the present paper, data are presented to show that among the lake Opeongo whitefish there are two distinct groups of mature fish. The remainder of the paper is devoted to a comparison of these two groups as to morphology, growth rate, and vertical distribution during the summer.

## ACKNOWLEDGMENTS

This work was done in the Ontario Fisheries Research Laboratory of the Department of Biology, University of Toronto, which also receives financial aid from the Ontario Department of Game and Fisheries. The Laboratory is fortunate in having the co-operation of the Ontario Forests Branch in Algonquin Park. The support of Mr. F. A. MacDougall, as Superintendent of Algonquin Park, particularly facilitated the present work.

I am pleased to acknowledge the helpful guidance of Professor J. R. Dymond.

I am indebted to all members of the Ontario Fisheries Research Laboratory for assistance in the present work, especially to the director, Professor W. J. K. Harkness, and I am extremely grateful to Dr. F. E. J. Fry, whose criticisms and advice I have frequently sought.

Dr. M. A. Ross, Assistant Professor in Biometrics, was kind enough to assist me with the mathematics of co-variance.

## DESCRIPTION OF LAKE OPEONGO

Lake Opeongo ( $45^{\circ} 40' N$ ,  $78^{\circ} 25' W$ ) is the largest lake in Algonquin Park, with an area of 20.5 square miles. It is composed of the North, East, and South Arms, three separate basins which are approximately equal in area and joined by restricted channels.

The shores are, in general, wooded to the high water line. Most of the shoreline is granitic rock, but a few sand beaches are present and protected bays show bog conditions. Rough observations indicate that while sand or rock bottoms may be encountered down to 15 feet, the greatest part of the lake bottom is a black, sticky, loose muck into which a sounding lead readily sinks as much as 6 inches. The water is soft, brown in colour, and low in transparency.

## METHODS OF OBTAINING FISH

The whitefish used in the following studies were taken by several different means, the most important of which was the use of gillnets ranging in size from 1 to 5 inches inclusive, stretched mesh.

While a few whitefish were taken in the years 1936 and 1938, the first extensive fishing for whitefish was begun in 1939. In that year nets were set in both the East and South arms to obtain specimens, especially large fish (over 30 cm.). In 1940, further specimens were collected, but most effort was placed on an intensive study of vertical distribution of the whitefish throughout the growing season. This study was made in the South arm only.

A variation of the gillnet described by Fry (1937) was used in 1940 to catch the smallest fish. It consisted of milliner's net of approximately  $\frac{1}{2}$ -inch mesh hung between two  $1\frac{1}{2}$ -inch mesh gillnets and will be referred to as "the veiling net."

Besides the whitefish taken in gillnets, a few were taken in fyke nets, and some were also obtained from stomachs of lake trout, *Cristivomer namaycush* (Walbaum) and burbot, *Lota maculosa* Le Sueur. Finally, a few large fish which were caught by anglers while trolling for lake trout were obligingly loaned long enough for the required measurements to be taken.

The number of fish taken by gillnets completely overshadowed the combined numbers taken by these other means.

## SIZE DISTRIBUTION

### *Mature Fish*

Early in the investigation, it became obvious that the size distribution of the fish taken was distinctly bimodal. However, it was known that the gillnets used in the investigation tended to select two groups of fish because of the sizes of mesh used (table 18, p. 61 for mesh sizes). In particular, fish of the 17-20 cm. class were not well represented in the catches. Therefore, figure 1 was prepared showing the percentage of mature fish in each length group for all the fish taken in September, 1939.

This figure shows that apart from the absolute scarcity of mature fish over the range 13-20 cm., they are also relatively scarce within each length group in that range. It should be stated that the sexes are approximately equally represented in each of the two modes.

The bimodality is even more apparent when age is taken into



account (figure 6, p. 56). At age IV and age V<sup>1</sup> complete separation into two groups is exhibited. At age III, groups of mature fish are completely separated from one another, though immature fish are taken at intermediate sizes. At age II, the smaller group only is represented by mature fish.

If, then, age is taken into account, the mature fish taken in September, 1939, are seen to consist of two completely separated groups. These evidences of bimodality are further confirmed by a study of all other available specimens, the data for which are on file in the Royal Ontario Museum of Zoology.

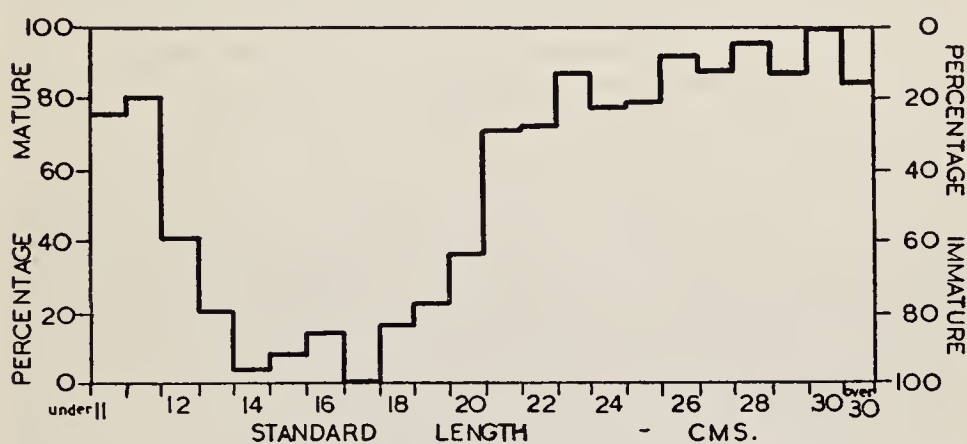


FIGURE 1.—Percentage of mature fish in each length group of all whitefish caught in September, 1939.

### *Immature Fish*

It is evident that a bimodality also exists in the percentage of immature fish. Thus, the smallest fish—which are not represented in figure 1, because they are too small to be caught—are all immature. The other mode occurs in the size range 13-20 cm. where a large proportion of the fish represented are immature.

### DEFINITION OF TERMS

In the present paper, the group of smaller mature fish are referred to as “dwarfs,” while the group of larger mature fish are

<sup>1</sup>A fish hatched in the spring of the current year is designated as “age I”; one which has completed a year of life and is now on its second year is designated as “age II”; and so on.

referred to as "mature normals." These terms are used for descriptive reasons only and do not imply that dwarfs are in any way abnormal or subnormal.

Since 75 per cent of the fish taken in 1939, which were less than 11 cm. long, were mature, it was assumed that all or almost all dwarfs had matured before reaching this size, and that the immature dwarfs were too small to be captured. Accordingly, it was considered that even the smallest immature fish taken belonged to the normal group. As will be shown later, there is a difference in growth rate between the two groups of fish, and evidence from the growth rate of the immature fish further strengthens the assumption that they would have become mature normals. These immature fish are, then, referred to as "immature normals." The immature normals and the mature normals are collectively referred to as "normals."

Eight immature fish of the size range 9-11 cm. were excluded from this definition of immature normals, as there was the possibility that they were immature dwarfs. Nineteen specimens taken in their first year in the veiling net were similarly excluded. In cases where these two groups were considered with other immature fish, the whole was referred to as "immatures."

#### MORPHOLOGICAL COMPARISONS

Populations of fish and other animals which have diverged sufficiently widely to be regarded as belonging to distinct species, subspecies, races, or varieties usually differ in morphological as well as physiological characters. In the case of fish, measurements and counts of various body parts are the structural characters usually found most useful in comparisons of closely related populations.

Before dealing with the actual morphological comparison of dwarfs and normals, a discussion of the effects of preservation will be presented, followed by a consideration of the morphological differences between sexes.

#### *Measurements Used*

In the present study, the following measurements were taken:

*Total length*—the distance from the tip of the snout to the fork of the caudal fin measured in inches.



*Standard length*—The distance from the tip of the snout to the posterior end of the vertebral column measured in millimetres.

*Weight*—taken in ounces for larger fish or grams for smaller fish. All weights were converted to grams.

*Head length*—The distance from the tip of the snout to the most posterior margin of the bony part of the operculum.

*Eye diameter*—the diameter of the uncompressed eyeball in a horizontal plane.

*Snout length*—the distance from the anterior margin of the orbit to the tip of the snout.

*Anal fin length*—the distance from the anterior base of the fin to the distal end of the longest ray.

*Pectoral fin length*—the distance from the middle of the base of the pectoral fin to the distal end of the longest ray.

*Caudal peduncle depth*—the minimum depth of the caudal peduncle.

The fish were weighed soon after capture on either a small balance or, in the case of larger fish, on a grocer's scales. They were then laid on a ruler to determine total length and immediately beside a ruler to determine standard length. The remaining measurements were taken with calipers while the fish were still fresh or after the fish had been preserved in formalin.

#### *Effect of Preservation on Body Measurements*

Since the detailed measurements of some fish were taken while fresh and of others after being preserved, it was necessary to determine the extent to which these measurements were affected by preservation.

Thirty-eight fish were measured when fresh and again after preservation for from one to four months. For each fish, the algebraic sum of the percentage differences between the two measurements was calculated. The deviation  $s$  of the individual measurements and the deviation of the mean  $sM$  were also obtained (table 1). No significant variation was found in head or anal fin lengths, but eye diameter and snout lengths decreased and caudal peduncle and pectoral fin lengths increased significantly. The

decrease in eye and snout probably represents a real shrinkage in the parts named. On the other hand, the apparent change in pectoral fin length and caudal peduncle depth is likely only the result of the fact that these parts are more rigid after preservation.

TABLE 1.—The effect of preservation on body measurements.

Part measured	s	Mean % increase and sM
Head length.....	$\pm 2.88$	$0.16 \pm 0.47$
Eye diameter.....	$\pm 7.03$	$-4.30 \pm 1.14$
Snout length.....	$\pm 8.13$	$-7.84 \pm 1.34$
Anal fin length.....	$\pm 3.53$	$0.87 \pm 0.59$
Pectoral fin length.....	$\pm 6.55$	$3.86 \pm 1.08$
Caudal peduncle depth.....	$\pm 3.98$	$1.68 \pm 0.65$

The deviation of measurements may be in part associated with differences in measuring the same specimen from one time to another. To determine this variation, twenty-five fish, which had been preserved in formalin for some time, were measured, returned to the formalin and measured again several days later. The average difference between successive measurements with its deviation, as well as the deviation of individual measurements, is shown in table 2. The algebraic sum of the percentage difference between the first and second measurement is seen to be practically zero.<sup>2</sup>

TABLE 2.—The apparent increase in length of body proportions in two successive measurements.

Part measured	s	Mean % increase and sM
Head length.....	$\pm 1.76$	$-0.47 \pm 0.35$
Eye diameter.....	$\pm 4.85$	$-0.16 \pm 0.97$
Snout length.....	$\pm 8.30$	$-1.96 \pm 1.66$
Anal fin length.....	$\pm 3.08$	$0.54 \pm 0.62$
Pectoral fin length.....	$\pm 1.98$	$0.13 \pm 0.69$
Caudal peduncle depth.....	$\pm 4.08$	$-0.04 \pm 0.82$

<sup>2</sup>Notice the great difference in deviations in the differences of measurements of pectoral fin length and eye diameter between fish measured fresh and again after preservation. Preserved specimens are more rigid than fresh specimens, so successive measurements on the former would be expected to vary less than successive measurements on the latter.

In the measurements used in the subsequent discussion, suitable corrections have been applied to eye diameter, snout length, and pectoral fin length, the preserved fish being taken as the standard. Although a correction of caudal peduncle depth is indicated, the size of such correction is negligible and has not been applied.

### *Difference between Sexes*

Frequently in this type of comparison, males and females are found to differ in body characters. It is, therefore, necessary—particularly after they reach sexual maturity—to compare males and females in each of the three categories (dwarfs, immature normals, and mature normals) and over the whole size range to see whether or not males and females are the same in body characters.

To make such a comparison, the average size of the part was calculated in each centimetre class for each sex of a given category. These averages were then expressed as fractions of the corresponding average standard lengths. The catch of September, 1939, only was used, as it represented a complete series. The differences between the averages of the two sexes were recorded and, from these,  $t$  values were calculated (Fisher, 1936, p. 127) and the corresponding  $P$  values were obtained from Fisher's table IV and are shown in table 3.

Since a value of  $P$  greater than 0.05 is considered to indicate no significant difference, it is apparent that—excepting pectoral fin length and weight of normals—there is no significant difference between body measurements of males and of females. In the case of the pectoral fin the difference represents only 4 per cent of the actual values. The fact that the females weigh about 2 per cent more than the males—the difference being between the levels of significance—is to be expected, since ovaries weigh more than testes. These differences are slight and will be disregarded in the consideration of body measurements.

### *Fish Used in Relative Growth Studies*

Table 4 shows the number of specimens used in the relative growth studies of each sex and of various sizes among the immatures, mature normals, and dwarfs. No mature fish are recorded in the

TABLE 3.—Values of “P” obtained in tests of significance of the differences between body measurements of males and of females of corresponding sizes.

	No. of groups	Head length	Eye diameter	Snout length	Anal fin length	Pect. fin length	Caud. ped. depth	Weight
Dwarfs.....	4	0.33	0.47	0.15	0.08	0.21	0.06	<0.9
Immature normals.....	16	0.22	0.10	0.31	0.28	0.20	0.42	0.7
Mature normals.....	15	0.79	0.48	0.12	0.24	>0.01	0.42	0.04

15 cm. group, which lies between dwarfs and normals. Of the ten fish measured in this group, five were interpreted as age III normals, which had just begun growth for the year; three might have been age IV dwarfs; and for two, growth data were lacking. In view of the possible doubt as to whether members of this group were dwarfs or normals, they were not used in this study. Two age III mature fish of the 13 cm. class taken early in the season were considered to be normals and were omitted. Excepting these cases, all the fish measured are recorded in table 4.

The slight predominance of males among the dwarfs (60:40) and among the mature normals (61:39) should be noted. The small proportion of males (38:62) among the immatures less than 20 cm. is probably more apparent than real, since an ovary can be distinguished from an undifferentiated gonad at an earlier stage than can a testis and the sex of 44 per cent of these fish could not be determined. The sex ratio among immatures 20 cm. and over is 50:50.

#### *Morphological Comparisons*

The usual procedure in studies of this kind has been to divide the measurement of a body part by the standard length and compare the resulting quantities for consistent differences. This has certain limitations, since the proportion of certain body parts to standard length varies with size. Thus, it cannot be properly used in the present work, since by definition mature dwarfs cannot be of the same size as mature normals. Of course, it would be legitimate to compare immature normals with immature dwarfs, but unfortunately, only a negligible number of immature dwarfs, if any, have been taken.

This difficulty was overcome as follows: first, as proposed by Huxley (1932) the logarithm of the part measured was plotted against the logarithm of body length (figure 2). Since several hundred specimens are represented, the average sizes of body parts at different standard lengths were plotted instead of all the individual points. These averages were calculated for each of the three categories dwarfs, immature normals, and mature normals.<sup>3</sup> In

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<sup>3</sup>These data are on file in the form of tables in a Thesis deposited in the library of the University of Toronto.

TABLE 4.—Synopsis of the numbers of fish used in the relative growth studies.

Cm. class	Immatures			Normals		Dwarfs	
	♂	♀	Sex not determined	♂	♀	♂	♀
5			1				
6			2				
7			13				
8			5				
9			5				
10		1	1			10	4
11	1	2	8			19	15
12	5	15	31			11	11
13	14	30	48			11	7
14	17	29	37			7	1
15	12	24	18				
16	9	10	9	4	1		
17	8	10	3	1	0		
18	8	11	2	1	0		
19	13	13	1	3	5		
20	8	3		2	4		
21	8	8		11	14		
22	6	12		19	21		
23	8	8		29	21		
24	4	10		36	19		
25	5	3		33	11		
26	4	2		23	10		
27	2	1		12	7		
28	1	1		12	4		
29	1	3		11	8		
30	0	1		6	5		
31	5	2		4	0		
32	1	0		0	3		
33	2	0		0	1		
34	1	1		1	1		
35	0	0		1	1		
36	1	1		1	0		
37		0		1	0		
38		0		1	0		
39		1		0	0		
40				3	1		
41				2	1		
42				3	1		
43				1	1		
44				0	1		
45				1	0		
51					1		



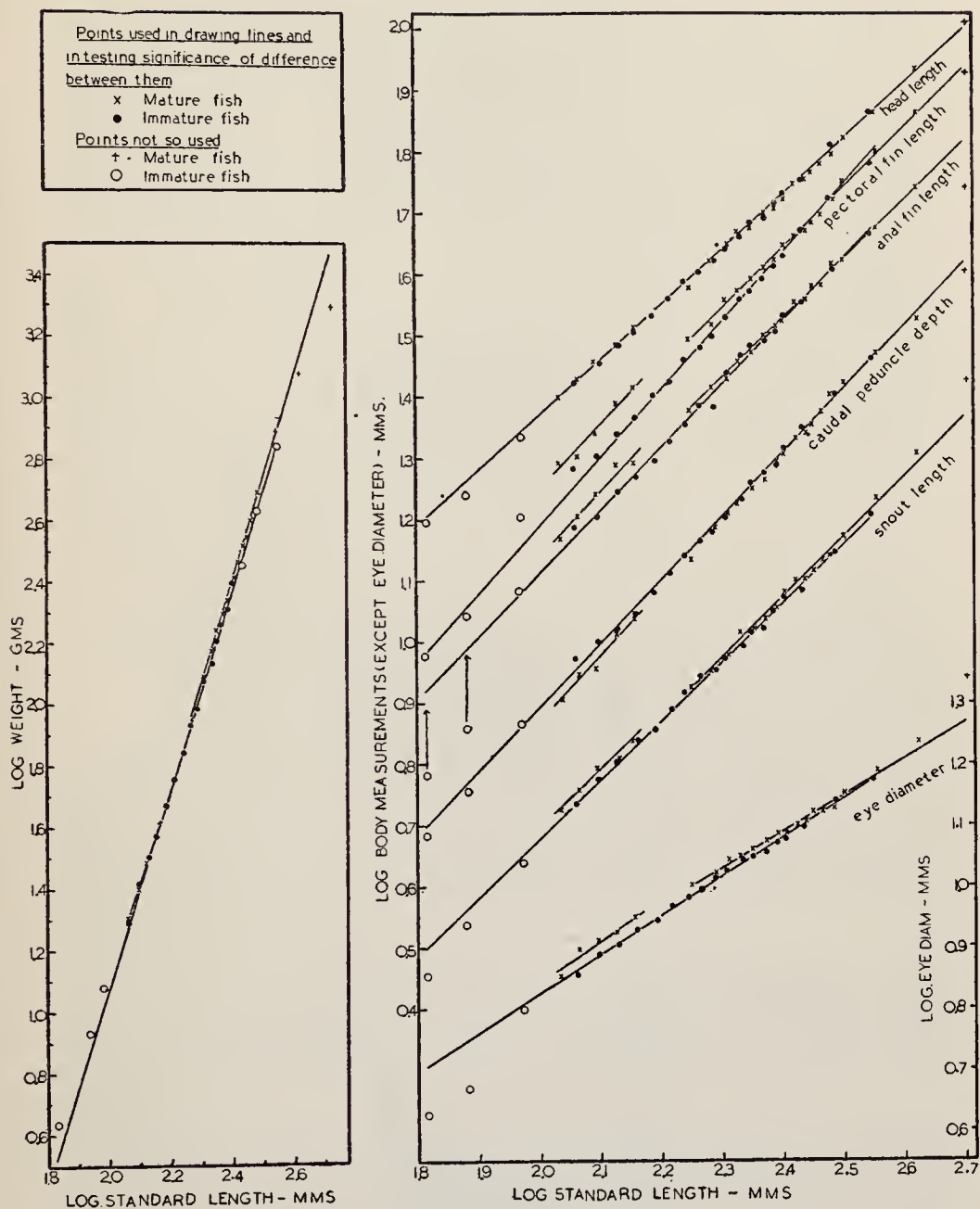


FIGURE 2.—Logarithms of body measurements plotted against logarithms of standard lengths. The lines are fitted from the formulae given in table 5.

TABLE 5.—Equations of the best straight lines through the points in figure 2. (E is the expected value of Y.)

	Dwarfs	Mature normals	Immature normals
Head length.....	E = 0.89X-0.41	E = 0.90X-0.44	E = 0.91X-0.4
Eye diameter.....	E = 0.68X-0.52	E = 0.59X-0.33	E = 0.64X-0.44
Snout length.....	E = 0.96X-1.22	E = 0.99X-1.30	E = 0.96X-1.24
Anal fin length.....	E = 1.07X-0.99	E = 0.95X-0.75	E = 1.03X-0.94
Pectoral fin length.....	E = 1.06X-0.87	E = 0.98X-0.71	E = 1.11X-1.04
Caudal peduncle depth.....	E = 1.04X-1.22	E = 1.04X-1.18	E = 1.04X-1.18
Weight.....	E = 2.89X-4.66	E = 3.28X-5.47	E = 3.18X-5.27



general, the intervals taken were centimetre classes, but in some cases several centimetre classes were grouped to bring the number of specimens on which the average was based to ten or more. Males and females were considered together in all cases. Information on sex ratio in this material was given in table 4. The eye diameter, snout length, and pectoral fin length were first corrected for differences between preserved and fresh measurements.

Inspection of figure 2 shows that a single straight line can be fitted to each series of points. The equations of the best straight lines—i.e., lines such that the sum of the squares of the deviations of the various points from each line is the least possible, assuming measurements of the body parts only are in error<sup>4</sup>—have been calculated as outlined by Snedecor (1938), and are shown in table 5.

It should be noticed that certain points are not used in drawing these lines. These points are:

- (1) Points based on too few specimens.
- (2) In the case of weights, averages based on values too divergent to be reliable.
- (3) Immature fish less than 11 cm. long which are not necessarily immature normals and which, as will be shown later (p. 43) are probably not representative of this size of fish.

Mathematical tests—as used by Mottley (1941)—have been applied to determine whether the lines representing dwarfs and mature normals are significantly different from each other, and again whether the lines representing immature normals are significantly different from those representing mature normals, with the results shown in table 6.

The most striking fact about the results of these tests is that *in no case is a definite difference in body proportions between dwarfs and normals demonstrated*. There is, however, a difference in intercept in the caudal peduncle which is between the levels of significance.

However, in the tests between mature and immature normals, there are three measurements in which there are significant differences, and one between the levels of significance. Thus, only head

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<sup>4</sup>In case of the length-weight relationship, the lengths only are assumed to be in error.

TABLE 6.—Results of tests of significance of differences between the lines shown in figure 2. The tests are for (1) Dwarfs versus mature normals; (2) Mature versus immature normals. *No* indicates no significant difference; *possibly* indicates the difference lies between the levels of significance; *yes* indicates a significant difference.

	DWARFS VS. MATURE NORMALS		MATURE NORMALS VS. IMMATURE	
	<i>Slope</i>	<i>Position</i>	<i>Slope</i>	<i>Position</i>
Head.....	No	No	No	No
Eye.....	No	No	No	Yes
Snout.....	No	No	No	Possibly
Anal.....	No	No	Yes	No
Pectoral.....	No	No	Yes	Yes
Caudal				
peduncle....	No	Possibly	No	No
Weight.....	No	No	No	Yes

length and caudal peduncle depth can be represented by the same lines. Snout length may possibly also be included, since it is between the levels of significance.

The reason for the difference in weights is evident, since the ripe gonad of the mature fish makes it slightly heavier than an immature fish of the same size. That there is a difference between the relative growth of body parts of mature normals and immature normals is not surprising, as it is frequently found in ichthyological work that there are changes in the relative growth of different parts when the fish reaches maturity. However, at first glance, this does not seem to fit the facts, since—except where the two lines are identical—the line representing immature normals does not intercept the line representing mature normals at its lower end.

It must be remembered, however, that averages rather than individuals are involved. Take for example, eye diameter. Each point used in calculating the best line is really an average of different sizes of eyes in fish of the same size. Should those fish with the large eyes tend to mature at a smaller size than those with small eyes, then the average eye size of those fish which remain immature would be less than would be the case if no fish had matured.

When, then, the effect of size difference between dwarfs and normals is eliminated as above, no significant difference is found between the two as regards the relative size of six measurements taken. On the other hand, in three of six cases, the matures differed

from the immatures with regard to the relative size of measured parts, which indicates a change in relative growth on reaching maturity.

### *Proportional Measurements*

The body measurements corresponding to lengths of a typical dwarf (126 mm.) and a typical normal (251 mm.)<sup>5</sup> were calculated from the respective equations. Proportional parts were worked out on the basis of these ideal measurements and are shown in table 7.

TABLE 7.—Proportional measurements of a typical dwarf (126 mm.) and of a typical mature normal (251 mm.) calculated from theoretical values.

	Proportional parts = $\frac{\text{Body measurements}}{\text{Standard length}} \times 1000$	
	<i>Dwarfs</i>	<i>Normals</i>
Head.....	228	212
Eye.....	64	49
Snout.....	49	47
Anal.....	138	134
Pectoral.....	178	174
Caudal peduncle.....	75	81

The most marked difference is in eye diameter, although a considerable difference is also seen in head length and in caudal peduncle depth. Differences of this kind have sometimes been regarded as sufficient to warrant the separation of populations so characterized into species or subspecies. Yet this difference results merely from a differential growth between the part and the whole which is the same in both groups. This example, then, serves to emphasize the fact that the use of proportional measurements is only justified when the fish to be compared are of the same size as well as of the same state of maturity. In cases where fish are not comparable in these respects, the method used in the present paper is the only safe one.

### *Scale Counts*

A count was made of the number of perforate scales in the lateral line wherever it was possible to do so. A recount on seven-

<sup>5</sup>These particular values were chosen because the logarithms were convenient for use.

teen specimens showed an average difference of  $0.12 \pm 0.43$  scales. No significant difference was found between counts taken on fresh fish and those taken on preserved specimens. Nor was a difference found between males and females in dwarfs, mature normals, or immature normals.

The average scale count for mature normals was 83.3 (335 fish), while the average for dwarfs was 77.3 (as the scales are easily rubbed off the small fish, only 19 dwarfs were suitable for scale counts). However, the chi-square test shows no significant difference between the scale count of dwarfs and of immature normals of the same size only.

It is interesting to note that the average scale count of normals over 15 cm. long is significantly greater than of normals less than 15 cm. long (82.0 and 80.7 scales respectively).

#### *Gill Raker Counts*

Gill raker counts were made on gill arches preserved from certain fish caught in 1940 and from thirty-three specimens preserved in 1939. The first gill arch was removed, pinned out, and the gill rakers counted under a dissecting microscope.

It is possible that more gill rakers may be observed in large fish than in small fish. Therefore, only immatures of the size 11-14 cm. inclusive were compared with the dwarfs.

These immature normals had an average gill raker count of  $27.4 \pm 0.22$  (46 specimens), whereas the dwarfs had an average count of  $25.4 \pm 0.14$  (63 specimens). The difference between these counts is highly significant.

It may be stated that the average gill raker count for all normals, regardless of size, was  $27.7 \pm 1.1$  (108 specimens).

#### *Vertebral Counts*

Vertebrae were taken from 117 dwarfs and 176 normals of similar size. The vertebrae were removed and counted at the time of capture, and counted again several weeks later. No significant difference was found between the first and second counts. Nor was a difference found between the number of vertebrae in the two sexes, nor between large and small fish in the normal group.



The comparison of vertebral counts of dwarfs and of normals is shown in table 8. The chi-square test has been applied to these figures and a  $P$  value of 0.80 obtained, which is not significant.

TABLE 8.—Comparison of frequency distributions of vertebrae counts in dwarfs and in normals.

	<i>Number of vertebrae</i>								
	56	57	58	59	60	61	62	63	Total
Dwarfs.....	—	6	14	47	28	20	1	1	117
Normals.....	2	8	13	59	60	27	6	1	176

### *Summary of Morphological Comparisons*

Dwarfs and normals do not differ significantly in the relative size of any of the six body parts measured nor in weight at comparable sizes. They do not differ in vertebral counts, but do differ significantly in scale counts and gill raker counts.

### RATE OF GROWTH

In the following section, data on both the general growth rate and seasonal growth of dwarfs and of normals are presented.

### *Methods*

In the growth studies, scales were removed from directly under the dorsal fin and between it and the lateral line. If scales were not available from this region, they were taken from some other part of the fish, but such scales were used only to estimate the age at capture and were not used in calculations of the size of the fish at the time of formation of previous annuli. The scales were preserved dry, and later about four from each fish soaked overnight in water, rubbed between the thumb and forefinger to remove dirt and mounted on a glass slide in Defauré's solution.<sup>6</sup>

The slides were then placed on the stage of a Leitz Edinger pro-

<sup>6</sup>Formula for Defauré's solution:

Gum Arabic.....	30 gms.
Chloral Hydrate.....	50 gms.
Glycerine.....	20 cc.
Distilled water.....	50 cc.
Cocaine Hydrochloride.....	0.5 gms.

jector which projected an image of the scale magnified about 18 diameters down on a white surface, placed on top of a table. The method is standard procedure and is reviewed by Van Oosten (1928).

Although false annuli seem to be present in certain specimens, it is felt they were distinguishable from true annuli by virtue of their position. A preliminary study of the characteristics of these false annuli was made on a series of scales from fish caught throughout the whole growing season of 1938.

At the same time as the age was determined, the two points at which the annuli in the projected image cut the antero-posterior diameter were recorded on filing cards as described by Lea (1915). Later these filing cards were used to calculate the size the fish had been at the time of formation of each previous annulus. This calculation was done by means of a calculator developed by Fry (1943).

The use of this calculator involved as a preliminary step the construction of a graph showing the relation between the logarithms of scale diameters and the logarithms of body lengths less the length at time of scale formation. To construct this graph, the average length and average scale diameters within each age class were determined for all available fish caught in 1939, and in addition, for age I fish caught in 1940 (table 9).

These data were plotted on an arithmetic grid and extrapolation showed the size at scale formation to be approximately two centimetres. Knowing this, figure 4, showing the relation between the logarithm of scale diameter and the logarithm of body length less two centimetres, was made. Since a straight line fits these points, it is assumed that the length at time of scale formation was two centimetres.

Dwarfs fall on the same curve as the normals, so this curve has been used in calculating the sizes of dwarfs as well as of normals at previous ages.

It will be noticed that the lowest point in figure 4 falls too far off the curve to be the result of chance alone. However, it was found that the scale counts of the individuals making up this group were abnormally low (average  $72.0 \pm 0.8$  as compared with 80.7 in normals and 77.3 in dwarfs). The fact that this group does not



A



B

FIGURE 3.—Two age IV lake Opeongo whitefish scales, each magnified nineteen times. A from mature dwarf ♀, 128 mm.; B from immature normal ♂, 200 mm.





truly represent the population as a whole is not altogether surprising, since these fish were taken only under special circumstances, namely at a definite time of year in a special type of gear, and in one location; hence the possibility of selection is strong.

TABLE 9.—Average body lengths and average scale diameters in each age group. All fish were taken in 1939 except the age I fish which were taken in 1940.

Age	NORMALS			DWARFS		
	Number of specimens	Average standard length mms.	Average scale diameter mms.	Number of specimens	Average standard length mms.	Average scale diameter mms.
I...	13	78	1.5	3	109	2.0
II...	63	133	2.5	19	118	2.2
III...	39	156	3.0	15	128	2.4
IV...	41	218	4.5	2	133	2.4
V...	57	242	5.1	1	134	3.7
VI...	139	249	5.2			
VII...	41	250	5.2			
VIII...	62	258	5.4			
IX...	42	273	5.7			
X...	14	315	6.8			
XI...	7	391	8.4			
XII...	3	377	8.0			
XIII...	2	403	8.4			
XIV...	1	456	9.7			

Having calculated the sizes at previous ages, the average size for each year class at each previous annulus, for the specimens caught in the years 1938, 1939, and 1940, was determined. Only fish taken after July 1, in the case of normals, or July 15 in the case of dwarfs, were used, since some fish taken before these dates had not commenced growth for the year. These data are presented in table 10.

### *Lee's Phenomenon*

Since many fisheries investigators have encountered "Lee's phenomenon," it seemed desirable to see if it also appeared in this set of data. Lee's phenomenon is a condition in which the length

at a given age calculated from older fish is found to be less than the length calculated from younger fish.<sup>7</sup>

Inspection of table 10 shows no evidence of Lee's phenomenon. In fact, there seems at first glance to be an opposite tendency, namely, that the lengths calculated from older fish tend to be *greater* than lengths calculated from younger fish. This impression

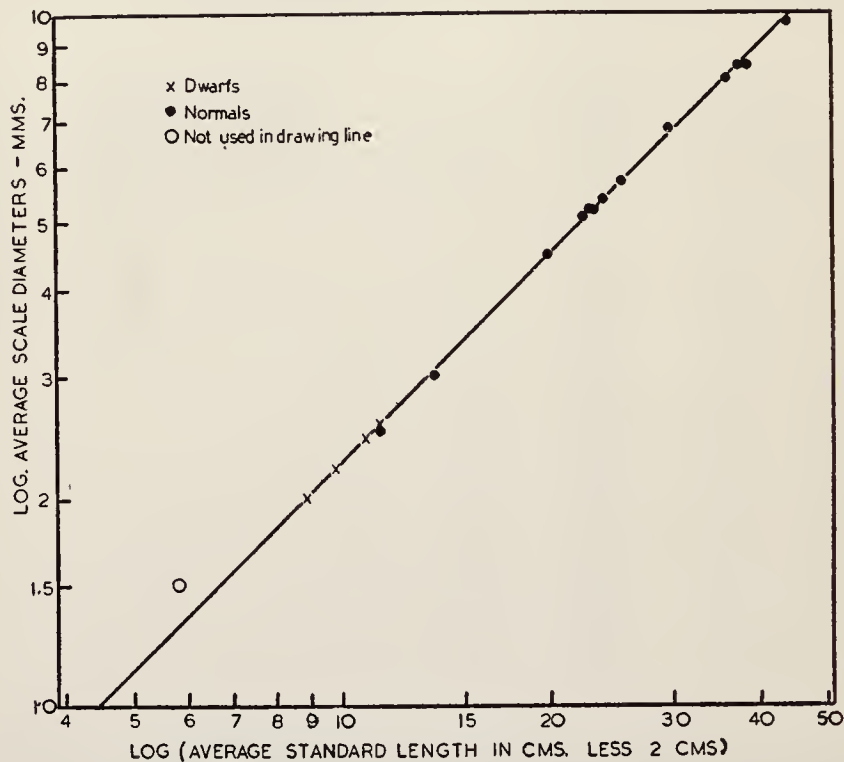


FIGURE 4.—Logarithms of average scale diameter in each age class plotted against logarithms of {(average standard lengths) – (length at time of scale formation)}. See table 9 for data.

is the result of taking into consideration the oldest fish whose numbers are inadequate. For the present, then, only those year classes for which fifty or more specimens are available will be considered—i.e., the 1931 and subsequent year classes. In these

<sup>7</sup>Lee (1912) states: "We have determined the prevalence of an apparent change in the growth rate from the calculated values of lengths of fish of different age at corresponding years of their existence, by which it appears that in older and older fish less growth is attained in each year of their existence."



year classes, although average lengths are seen to vary from year to year, no marked trend is apparent.

### *Comparison of Calculated Lengths*

In table 10, in those cases where the numbers of specimens were large enough, standard deviations of the means have been worked out. These data made it possible to compare calculated lengths of fish of the same age of the same year class caught in different years. For instance, the average calculated length of those age I fish of the 1936 year class caught in 1938, were compared with the average calculated length of those age I fish of the 1936 year class caught in 1939. Similar comparisons of the average calculated lengths of the age I fish of the 1936 year class were made between fish caught in 1939 and those caught in 1940, and between those caught in 1938 and those caught in 1940. Three more such comparisons were made among the average calculated lengths of fish at age II in the 1936 year class and one comparison between the average calculated lengths of fish at age III in the 1936 year class. In the 1937 year class, four comparisons were made between average calculated lengths and in the 1938 year class one comparison. Of these twelve comparisons, only one showed a significant difference while three were between the levels of significance.

The calculated lengths of fish of the same age caught in the same year which belonged to different year classes were also compared. For example, calculated length at age I of fish of the 1939 year class caught in 1940 was compared with the calculated length of age I fish of the 1938 year class caught in 1940. Similar comparisons were made between the other combinations of 1936, 1937, 1938, and 1939 year classes at age I caught in 1940. Comparisons were also made among the fish caught in 1940 between the average calculated lengths at age II of representatives of the 1936, 1937, and 1938 year classes, and at age III of members of the 1937 and 1938 year classes. Similar comparisons were made among the fish caught in 1939. The ten comparisons among the fish caught in 1940 showed 60 per cent significantly different. Thirty-eight similar comparisons among the fish caught in 1939 showed

59 per cent significantly different. The various data comparing calculated lengths at each age are summarized in table 11.

TABLE 11.—Summary of the results of comparisons between average calculated sizes of fish of comparable ages.

Group within which comparisons are made	No. of comparisons	% signif. different	% between levels of significance	% not signif. different
Fish caught in 1940....	10	60	20	20
Fish caught in 1939....	83	59	13	28
The same year class caught in different years.....	12	8	25	67

From these data, it is evident that although the average calculated length at any given age varies from one year class to another, the average calculated length at the formation of a given annulus within any year class is predominantly the same, in spite of a difference in age when the scales were taken.

Further, in table 10, no marked tendency was found for lengths calculated for a given age of fish of consecutive year classes from specimens taken in the same year to be more nearly identical than those for year classes further separated, as would be the case if Lee's phenomenon were involved.

### *Older Fish*

The twenty-eight fish of year classes previous to the 1931 year class—which were disregarded above during the discussion of the 995 specimens in the other year classes—will now be considered. To throw further light on the apparent larger-than-average calculated previous sizes of these fish, such sizes for fish taken in 1936 are presented in table 12, which should be compared with table 10. In any given age class, the difference between calculated lengths of fish taken in 1939 is not more different from those taken in 1936 than would be expected with so few specimens. Thus, such fragmentary evidence as is at hand indicates that the fish in the earlier year classes taken during this study actually were bigger than those in later year classes at any given age.

There is reason to believe that some years promote more rapid growth than other years. It seems possible that the years 1926, and



TABLE 12.—Average calculated lengths of normals from lake Opeongo in 1936.

Year class	Number of specimens	Length at end of year in millimetres							
		I	II	III	IV	V	VI	VII	VIII
1928	4	122	165	194	214	236	249	260	228
1929	2	109	142	168	186	199	211	225	
1930	3	115	146	171	190	205	220		
1931	4	108	136	154	166	179			
1932	3	107	142	164	177				



1927 promoted growth well above the average, while 1928, 1929, and 1930 were also good years for growth, though not quite so good. Perhaps this better growth is connected with the fact that the lake had been fished commercially during the Great War, which would tend to lessen competition in the years immediately subsequent to this.

There is also the possibility that those fish which grow fastest are most viable. If this happens to be the case, we can consider these oldest fish as a selected group from which the shortest lived—i.e., the slowest growing—have disappeared, leaving those which have always grown fastest. Evidence in support of this is gained from the fact that dwarfs grow more slowly than normals and live for a shorter time.

A third possibility is that net selection has produced this result. It should be remembered that a special effort was made in 1939 to secure the largest whitefish. It is thus quite possible that among the biggest fish, the average size of the fish taken was greater than the average size of fish of the same age in nature.

#### *Dwarfs*

Lengths at different ages have been similarly calculated for the dwarfs and are presented in table 13. In this case too few specimens are present to make good comparisons, but there is no sign of any trend for the calculated lengths to be influenced by whether an old fish or a young fish is used.

#### *Summary*

In summing up the above, it can be said that *there is no evidence of Lee's phenomenon within the whitefish population of lake Opeongo.*

#### *Average Growth Histories of Different Sizes of Fish*

In connection with Lee's phenomenon, an hypothesis known as "the law of compensation of growth" was developed. This hypothesis states that fish which grow relatively fast when young grow relatively slowly when they become older, while fish which grow slowly when young, grow relatively fast when older. The growth of a number of species of fish has been considered to conform to this law, among which are the whitefish. Van Oosten (1939) says: "The 'law of compensation of growth' was found to apply to Lake Huron whitefish."

TABLE 13.—Average calculated lengths and sM of dwarfs from lake Opeongo in the years 1938, 1939, and 1940.

Year class	Year of capture	Number of specimens	Length at end of year in millimetres				
			I	II	III	IV	V
1934	1938	16	94±1.2	117±1.2	117±1.2	123±1.2	
1935	1938	30	90±1.5	111±1.1	119±1.5		
	1939	2	96	101	120	128	
	1940	1	89	104	117	123	126
1936	1938	21	98±1.4	115±1.2			
	1939	15	93±2.1	112±1.2	123±1.9		
	1940	3	98	111	122	130	
1937	1939	18	88±1.0	111±1.0			
	1940	15	87±1.6	107±1.3	116±1.6		
1938	1939	3	77				
	1940	39	89±1.2	108±0.8			
1939	1940	4	76				

To test the validity of this hypothesis among Opeongo whitefish, all the age VI normals caught in September, 1939,—when growth was known to be finished for the year—were divided into three groups of equal numerical strength, one group representing the largest fish when captured, one those intermediate in size, and one the smallest fish taken. Within each of these groups, the average size at each previous age as well as the average size at capture was calculated. These data, and the increments of growth in each year derived from them, are shown in table 14.

It is apparent that those fish which are largest when captured have always been largest, while those fish which are smallest when captured have always been smallest.

To test this hypothesis further, the age VI normals were again divided into three lots, this time on the basis of size at the end of the first year. The average length at each subsequent year of life was calculated within each of these groups. These averages are given in table 15.

TABLE 14.—Growth history of fish of the 1934 year class comparing past growth histories of fish of different average sizes at the time of capture. All fish taken in September, 1939.

	Size group	No. in group	End of year					Size at capture
			I	II	III	IV	V	
Size at end of year in mms.	188-237	45	106	137	158	182	205	223
	237-254	46	107	140	168	201	227	245
	254-316	45	107	142	178	222	257	282
Increments of growth in mms.	188-237			31	21	24	23	18
	237-254			33	28	33	26	18
	254-316			35	36	44	35	25

TABLE 15.—Growth history of fish of the 1934 year class, comparing average subsequent growth of three groups of fish divided on the basis of size at the end of the first year. Fish caught in September, 1939, only were used.

	Size group	No. in group	End of year					Size at capture
			I	II	III	IV	V	
Size at end of year in mms.	93-104	45	100	135	164	198	228	246
	104-110	46	107	140	170	203	230	250
	110-125	45	114	143	167	203	233	250
Increments of growth in mms.	93-104			35	29	34	30	18
	104-110			33	30	35	27	20
	110-125			29	24	36	30	17

A study of this table shows that the group which is largest in their first year tends to be always largest, that of medium size to be always medium size, and the smallest to be always smallest.

A consideration of the increments of growth shown in table 14, would indicate that the fish which are largest when captured have always grown at a greater rate than have the fish which are smallest when captured. On the other hand, the increments of growth shown in table 15, indicate that each of the three groups tends to

add equal increments in a given year. That is, those fish which were largest on the average at the end of the first year do not grow at a different rate from those fish which on the average were smallest at the end of the first year. Rather, they maintain only the average difference in size reached at the end of the first year.

This paradox results from the fact that there is considerable variation among individuals comprising the average. Hence, one unusually good year of growth would put a fish in the largest size when caught, despite a moderate size at first. The fish of large size, then, would tend to be fast growing fish. On the other hand, fish which are larger than average at the end of their first year will be composed of individuals, some of which will grow faster, some slower, in any subsequent year. But, in general, an average rate of growth will be maintained.

Additional data showing growth histories for three different sizes of fish in the 1932, 1933, and 1935 year classes, all of which show the same thing, are on file.

*Correlation between Growth in the First Year and in Subsequent Years.*

The coefficients of correlation have been calculated for the relation between growth in the first year and that of the same fish in the second, fourth, sixth, and eighth years, using all available specimens. These correlation coefficients are shown in table 16.

TABLE 16.—Summary of the results of testing correlations between increments of growth in the first year and that in the second, fourth, sixth, and eighth years.

Between	Number of specimens	Coefficient of correlation	"P" of coefficient of correlation
I and II.....	695	-0.07	0.08
I and IV.....	454	-0.38	0.47
I and VI.....	207	-0.15	0.03
I and VIII.....	85	-0.017	0.88

In two cases the correlation is definitely not significantly different from zero; in another, it is between the levels of significance; and in the last, it is much smaller than would be expected if the law of compensation of growth had any bearing in this case. There is no evidence of a negative correlation which increases with a

greater separation between the years compared, as would be the case if there were compensation of growth in the lake Opeongo whitefish.

### *Average Growth Rate*

Average growth curves for normals and dwarfs are shown in figure 5 which was constructed by calculating a grand average for the length at each annulus from the data given in tables 10 and 13.

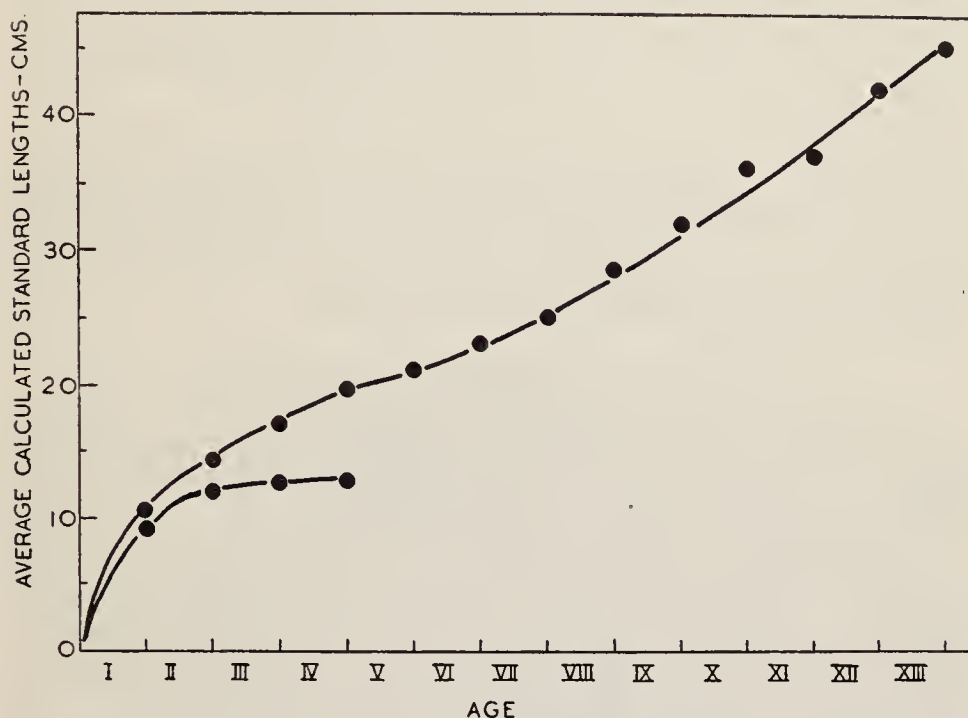


FIGURE 5.—General age length relationship for the lake Opeongo whitefish population.

This graph shows that dwarfs grow only slightly more slowly than normals for the first year, after which the difference becomes rapidly greater. The dwarfs almost cease growing after the second year at an average size of 125 mm.

The curve representing the average growth rate of normals is peculiar in that the growth rate appears to decline gradually after the first year until the end of the sixth year. Then apparently the growth begins to accelerate, becoming faster and faster throughout subsequent years. Pritchard (1931) and Fry (1937) found a similar



apparent increase in the growth of the cisco, *Leucicthys artedi* (Le Sueur).

It should be pointed out again that the oldest fish are few in number, and also seem to be larger at a given age than average members of the existing population. Although these few large fish do not affect the average when large numbers are used to calculate the size at a given age, yet as the numbers available for this calculation decrease, the effect of these few large fish becomes more marked, with the result that the average size at a given age is greater than would be expected from the trend among the fish when younger.

It may be considered, then, that it is not typical of this population to have a decrease in rate of growth extending over a period of years followed by an increase in growth rate. Rather, it would seem that the curve in figure 5 results from different growth rates in different years and in different individuals.

#### *Relation of Age to Maturity and to Death*

The histograms shown in figure 6 represent the frequency distribution of actual lengths of all fish taken in September, 1939. Blackened areas represent mature fish, clear areas immature fish.

The bimodality among mature fish mentioned before is quite apparent. It will be noticed that all normals taken were immature at age II. A few were mature at age III, and increasingly more at ages IV, V, and VI, until at age VII most of them were mature. All dwarfs shown were mature.

No dwarfs are shown which were older than age V.<sup>8</sup> Even at age V only two were represented. It seems, then, that most dwarfs die after age IV. Similarly, among the normals, the numbers rapidly decrease after age IX. This decrease in normals is even more marked if it is remembered that fish over 30 cm. were probably taken out of proportion to their numbers in the actual population, because a special effort was made to catch large fish in 1939.

It would seem, then, that dwarfs have an accelerated life cycle as compared with normals, they mature first, their growth slows down sooner, and death comes earlier.

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<sup>8</sup>An age VII dwarf was taken in 1940.



*Seasonal Growth*

Since a good series of fish taken from May to September inclusive, 1940, was at hand, it was possible to study the growth throughout the growing season. In so far as the scale increases in its antero-posterior diameter as a function of increase in length of the fish, a measure of the increase in antero-posterior diameter outside the last annulus may be used to give a measure of the rela-

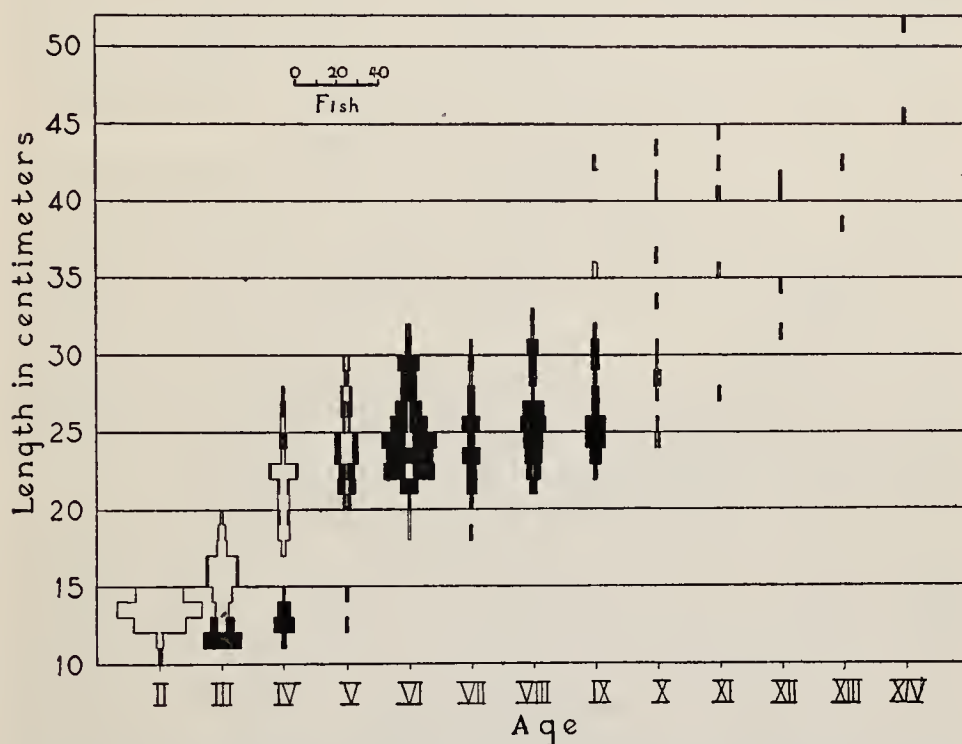


FIGURE 6.—Size, age, and state of maturity of fish taken in September, 1939.

The solid parts of the histograms represent mature fish, the light parts, immature fish.

tive increase in length of the fish between the time the previous annulus was formed and the time of capture.

To measure the increase along the antero-posterior diameter, beyond the last annulus, the scale was projected as described above, but in this case the image was magnified to about 42 diameters. Only scales taken from just below the dorsal fin were used in this study.

The average scale increment was calculated for each age group in each half-month for both dwarfs and normals. In general, at any given half-month within a year class, the scale diameter values tended to be bimodal, one mode representing dwarfs, the other normals. Some cases fell between the two modes, and the question of whether they were dwarfs or normals was settled by a consideration of the size of the specimen, state of maturity, age, and previous growth history. In a few rare cases, no definite decision could be made, and the data from such specimens were excluded.

The average increase of scale sizes within the age groups at half-month intervals is shown in the six lower panels of figure 7. From these, several conclusions may be drawn:

- (1) In general, the growth curve for normals differs markedly from that for dwarfs in any given age group. The normals not only grow faster, but also have a longer growing season.

- (2) Neither dwarfs nor normals show any evidence of growth before May 15.

- (3) In general, the older fish cease growing before the younger fish. The oldest fish have finished growing for the year by the end of July, while the youngest fish grow until September. In all cases, growth has practically ceased by the end of September.

Growth was also studied by a more direct method, namely, by taking the actual average sizes of the fish in each age group captured during each half-month. These data are also shown in figure 7. This method, though more direct, has an objectionable feature, in that the size of the fish at the start of the growing season is not taken into account. Therefore, accidental variation in size from the average may, to some extent, obscure average increases in length, especially where the number of specimens is small. In spite of this, it is evident that this method of studying seasonal growth leads to the same conclusions as were obtained by measuring increases in scale diameters.

Similar, though less complete data are available for scale growth in the year 1938. These data are on file in the Royal Ontario Museum of Zoology. They have been studied and found to show the same sort of seasonal growth as the 1940 data.

Thus whitefish in lake Opeongo grow rapidly for only a few months in the summer (May to September at most) after which

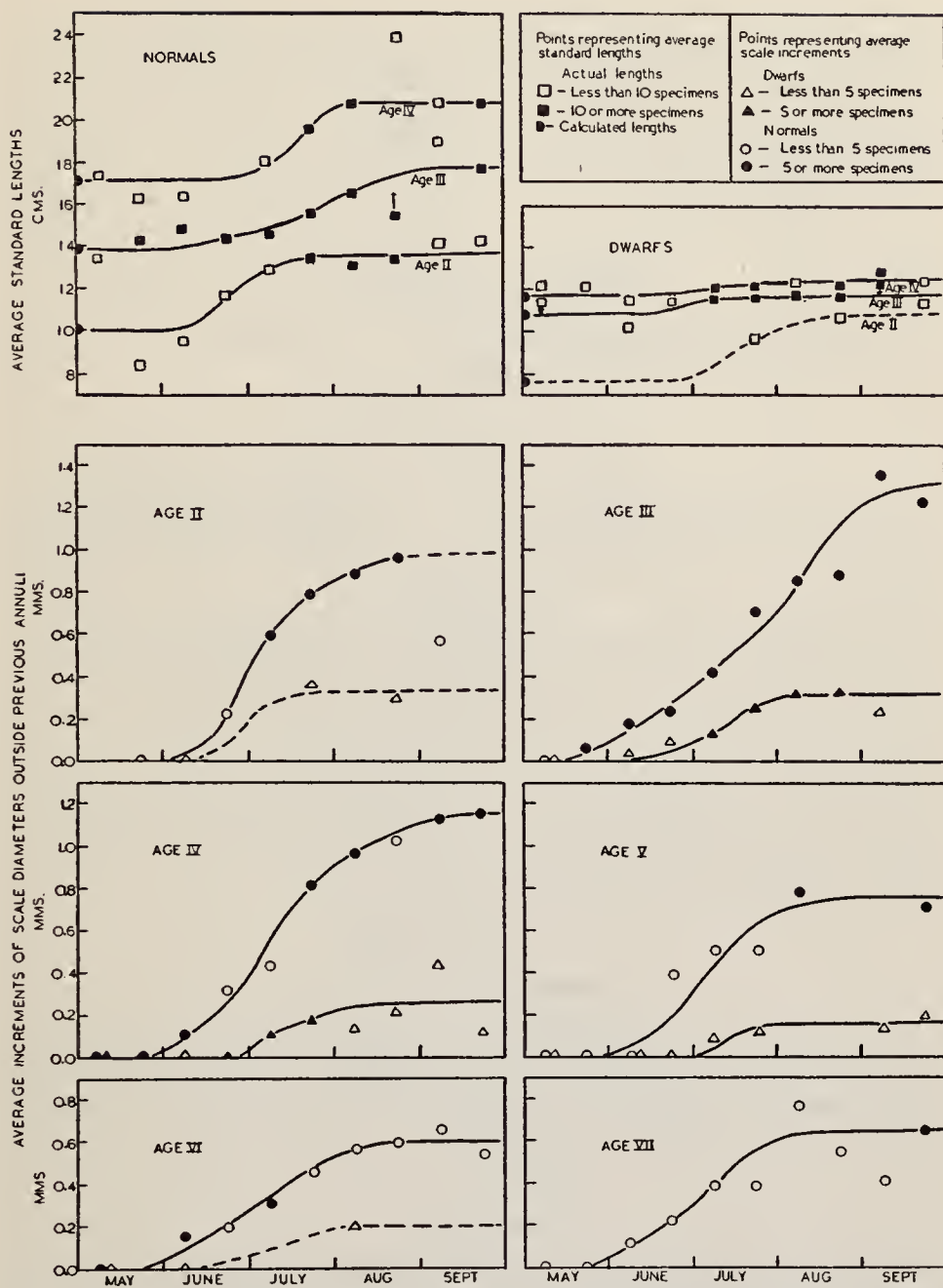


FIGURE 7.—Seasonal growth of lake Opeongo whitefish in 1940. The two upper panels are based on measurements of fish; the lower six on scale measurements.

growth ceases until the following May, when another burst of growth occurs. In general, the growing season lasts longer in younger fish than in older fish, and further, younger fish grow faster for each part of that time. Dwarfs grow for a shorter time than normals of the same age, and grow at a slower rate during each part of that time.

#### VERTICAL DISTRIBUTION

In 1940, the vertical distribution of the whitefish was studied, during the period May to September.

##### *Methods*

In this study, a graded series of gillnets was set at various depths. In general, the nets were set on the bottom of the lake, but four sets made in May were kited at various depths midway between bottom and surface.

In making a set, a locality known to be of constant depth was selected and soundings were taken frequently as the net was being set. If the soundings varied from the desired depth, the course of the boat setting the nets was altered as required. Thus, the depth at which the nets were set was kept within 5 feet of that desired, this depth in all cases being a multiple of 10 feet. The few sets which happened to exceed the range of plus or minus 5 feet have not been used in this distribution study.

##### *Grounds Fished*

Two general localities of lake Opeongo were sampled in this study, namely, Sproule bay and the south part of the South arm. The stations fished are shown in figure 8 and the amount of fishing at each station is shown in table 17.

##### *Gear Used*

Three gangs of nets, each consisting of six 50-yard nets of various sized mesh were used. These gangs are designated as: Gang 1, Gang 2, and Gang 3. The composition of these gangs is shown in table 18.

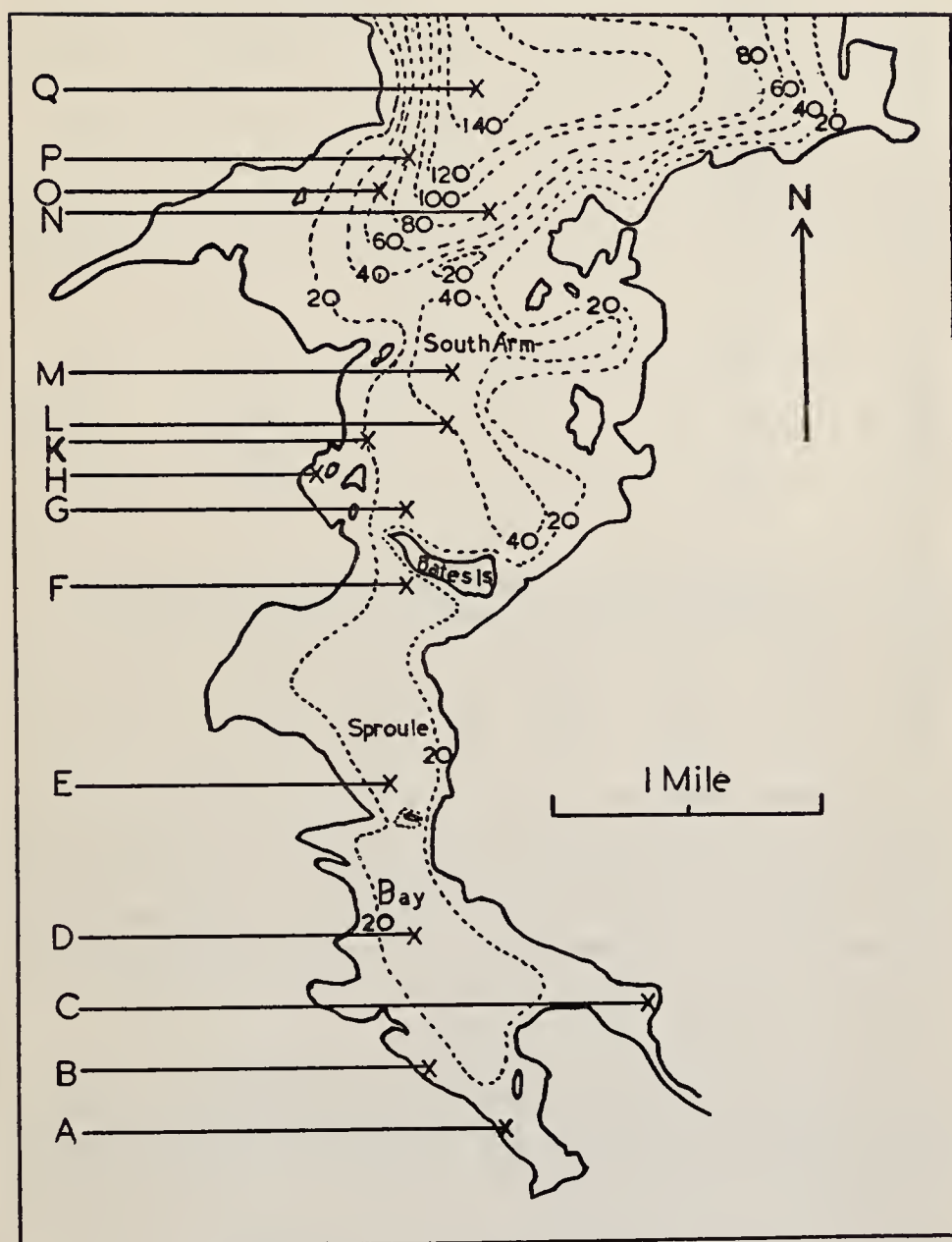


FIGURE 8.—Map of the south part of the South arm of lake Opeongo showing the stations fished in 1940. Contour lines are in feet. See also table 17.

TABLE 17.—The amount of fishing at the stations shown in figure 8.

Station	Depth in feet	No. of sets			Total
		Gang 1	Gang 2	Gang 3	
A	10	0	3	2	5
B	10	0	0	1	1
C	10	0	1	0	1
D	20	9	1	1	11
E	20	3	2	2	7
F	20	3	7	0	10
G	30	14	21	19	54
H	10	3	4	2	9
K	20	5	7	2	14
L	40	3	6	6	15
M	50	16	9	6	31
N	80	1	0	0	1
O	60	1	3	1	5
P	80	0	0	1	1
Q	140	0	0	1	1

TABLE 18.—The sizes of mesh (stretched) used in the gangs of gillnets fished in 1940. Number of yards of each sized mesh

Gang	1"	1¼"	1½"	2"	2½"	3"	4"	4½"
1	50	—	50	50	50	50	50	—
2	—	50	50	50	50	50	—	50
3	—	50	50	50	50	50	—	50

In addition to the nets listed in table 18, the veiling net was included with gang 1 from commencement of fishing until August 15, after which time it was fished separately. It should be noted that some fish were caught in the larger net protecting the veiling net, and these have not been kept separate from the general catch of Gang 1. However, the numbers so taken were negligible compared with the total catch of the gang.

On July 29, 50 yards of 4-inch mesh were substituted in Gang 2 for the original 50 yards of 4½-inch mesh which had become ragged. It is felt that this did not materially affect the efficiency of Gang 2.

Apart from these two changes, the gangs were fished as shown throughout the whole summer.

#### *Effect of Fishing More than One Night*

In general, nets were set one day and lifted the following day—i.e., were left out one night. However, sometimes it was necessary



to leave them for two or more nights before they were lifted. Hile (1935) and Tester (1935) have shown that gear left two nights catches little more on the average than the same gear lifted after one night. This principle was found to apply in the present study.

Fish in the nets were repeatedly attacked by predators—loons, lake trout, and burbot—to such an extent that it was not difficult to imagine them clearing the net during the daylight hours. The effect on the catch of increasing the number of nights fished is shown in table 19.

TABLE 19.—The effect of leaving nets more than one night.

No. of nights	Catch	No. of sets	No. per set	No. per night
1	822	131	6.3	6.3
2	196	29	6.7	3.4
3	12	5	2.4	0.8
9	1	1	1.0	0.1

It should be noticed that the total number of fish given in this table exceeds the number of specimens recorded as taken in 1940. This is because some of those recorded, although recognizable as whitefish remains, had been so mutilated that no other records could be taken from them.

It seems correct to consider that a gang which has fished continually for more than one night yields on the average the same number of fish as a gang which has fished only one night. In the following calculations on distribution, the number of sets has been taken as the basis for computing fishing effort rather than the number of nights fished.

#### *Relative Efficiency of the Gangs*

As mentioned above, three different gangs of nets were used in this investigation. Although these gangs were as nearly alike as circumstances allowed, there were differences in the state of repair of the nets, as well as slight differences in the sizes.

Gang 1, presumably because it contained a 1-inch mesh as compared with minimum sizes of  $1\frac{1}{4}$ -inch in the other two gangs, caught twice as many dwarfs per unit effort as Gang 2 and nine times as many dwarfs per unit effort as Gang 3. Per unit effort

Gang 1 and Gang 3 caught 10-15 cm. normals in about equal numbers, while Gang 2 caught about 50 per cent more than either of these. All three gangs were about equally efficient in taking larger fish.

Although the three gangs varied considerably in efficiency, the small number of specimens caught in each gang makes it advisable to lump all catches as if the gangs were of the same efficiency. The fact that the three gangs were fished at random with respect to depth, and that all were fished for the whole fishing season, makes this lumping less objectionable.

### *Seasonal Distribution*

All data were grouped and the average availability (i.e., fish per set) was calculated within each month and at each depth. These averages are represented graphically in figure 9, with normals in the left-hand panel and dwarfs in the right-hand panel. It should be noted that the scale of width for dwarf polygons is twice that for normals. Fish taken in Sproule bay are not included in these polygons, as they represent fish from a special locality.

On the whole, the seasonal distribution of dwarfs and normals is similar. Both are found at all depths fished in May. In June both groups had moved a little more inshore. The dwarfs differed from the normals in that the latter were taken in 10 feet of water while the former were not taken in any depth less than 20 feet. Neither was taken at depths greater than 40 feet during this month.

In July, both groups were taken in water from 20 to 50 feet deep. In August occurred the only striking difference between the distributions of dwarfs and normals. Here there was a concentration of normals at 30 feet and of dwarfs at 50 feet. The difference between these two concentrations was probably somewhat exaggerated by one exceptionally large lift of normals in 30 feet and one exceptionally large lift of dwarfs in 50 feet. In September, however, the two groups again showed similar distributions—namely, from 50 to 60 feet.

### *Relation of Vertical Distribution to Temperature*

Water temperatures were taken regularly in lake Opeongo in 1940 by means of a reversing thermometer. Data so obtained were

used to draw the isotherms between time and depth shown in figure 9.

In May when the water was of more or less uniform temperature throughout, fish were taken at all depths sampled. In June, when temperature differences were becoming established, dwarfs were found in water between  $7^{\circ}$  C. and  $14^{\circ}$  C., while normals were between  $7^{\circ}$  C. and  $16^{\circ}$  C. In July both groups were found in water from  $8^{\circ}$  C. to  $18^{\circ}$  C. In August, both groups ranged from  $7^{\circ}$  C. to

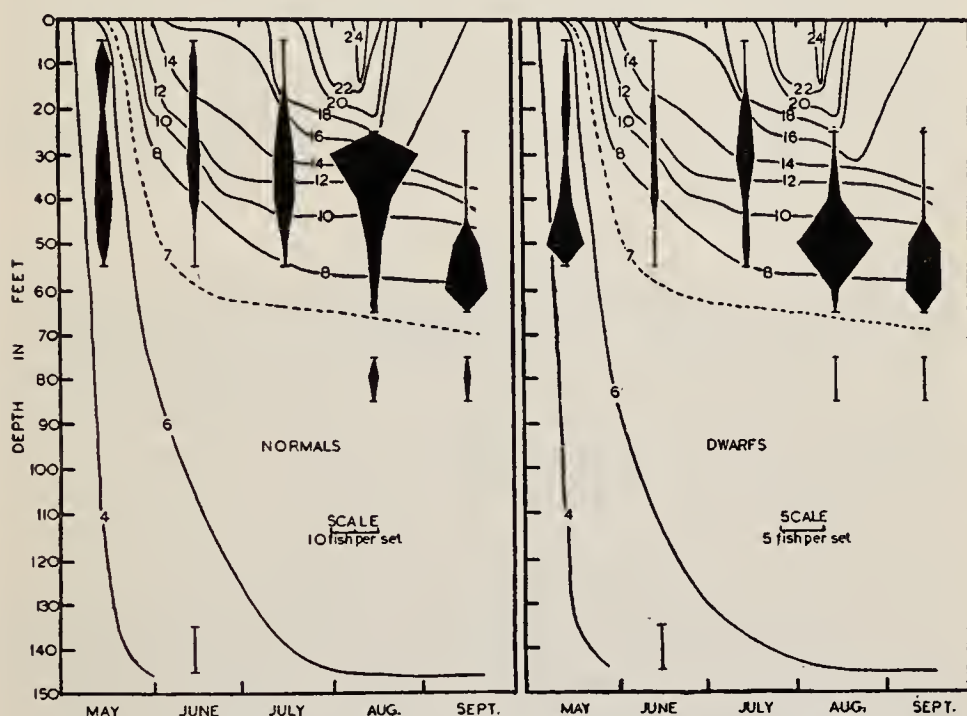


FIGURE 9.—Vertical distribution of whitefish (polygons) and temperature in degrees Centigrade (isotherms) in lake Opeongo, 1940.

$18^{\circ}$  C. but the normals were concentrated at about  $15^{\circ}$  C. and the dwarfs at  $9^{\circ}$  C. In September, both groups were taken only in the narrow temperature range  $7^{\circ}$  C. to  $10^{\circ}$  C.

It is apparent that these whitefish sought water warmer than  $7^{\circ}$  C. when it was available. The upper limit of the tolerated temperatures varied with the season. In July and August, the maximum tolerated temperature was  $18^{\circ}$  C. In September the maximum tolerated temperature dropped to  $10^{\circ}$  C.

*Significance of Vertical Distribution*

*A priori*, the difference in size between the dwarfs and normals might be considered to result from environment only. For, if it is assumed that the normals live in shallow water and the dwarfs live in deep water, the former would be exposed to higher temperatures than the latter, and would be expected to grow faster as a direct result. But as has been seen, August is the only month in which a pronounced difference in distribution is found, by which time—as shown in the growth studies—growth has practically ceased for the year. Further, there is no sharp separation between the ranges of the two even in this month. So, it seems apparent that the difference in size is not the result of the two groups living under different temperature conditions as a result of different vertical distributions.

## SUMMARY

Preliminary work on the lake Opeongo whitefish population indicates it is composed of two groups of fish which may be readily and completely distinguished by the size at which they mature. These two groups have been compared as to morphological characteristics, growth rates, and vertical distribution.

With respect to body proportions fish of the two groups follow the same laws of relative growth. There is no difference in vertebral counts, but the two groups do differ in gill raker and scale counts.

The lake Opeongo whitefish grow only during all or part of the period May to September. Young fish have a longer growing season than older fish, and normals have a longer growing season than dwarfs. Normals grow faster, mature later, and live longer than dwarfs.

No outstanding difference in vertical distribution between dwarfs and normals can be shown from the data available.

In the growth studies, no indication was found of Lee's phenomenon nor of the law of compensation of growth.

## DISCUSSION AND CONCLUSIONS

As a result of the present investigations, it can be definitely stated that the whitefish population of lake Opeongo is composed of two groups of fish. These groups are distinguished from each



other by the difference in size at which they mature, in rate of growth, in length of growing season, and in the number of scales and gill rakers.

Since both groups occur in the same habitats during the growing season, the above differences cannot be the direct result of environment. No evidence of intergradations between the groups was obtained.

Although the difference in size is a morphological difference, this is probably only an expression of physiological factors which cause one group to grow more slowly, to mature at a younger age, and to die sooner than does the other group. This seems to be a case of divergence in which two groups are well differentiated physiologically but are very slightly differentiated morphologically.

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